Simple Methods for Calculating Age-Based Life History Parameters for Stage-Structured Populations

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SIMPLE METHODS FOR CALCULATING AGE-BASED LIFE HISTORY PARAMETERS FOR STAGE-STRUCTURED POPULATIONS[1]

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Abstract. Stage-classified matrix models are important analytical and theoretical tools for the study of population dynamics; in particular, these models may be appropriate for populations in which survivorship and fecundity are dependent on size or developmental stage, populations in which the age of individuals is difficult to determine, and populations in which there are multiple types of newborns. Nevertheless, methods for analyzing the implications of a population's stage-transition matrix have been limited in comparison to methods available for age-structured models (life tables or Leslie matrices).

In this paper we show that all of the standard age-based measures of life history traits can be derived from a stage-transition model. By decomposing the transition matrix into separate birth, survival, and fission matrices we derive simple, direct formulas for age-based life history traits such as the discrete survivorship function, l_x, maternity function, f_x, mean age at maturity, and net reproductive rate, R_0, and also population parameters, including the stable age distribution, age-specific reproductive value, and generation time. These provide a common set of parameters for comparing age-structured and stage-structured populations or comparing populations with differently structured life cycles. In addition, we define four measures of age and life-span that summarize the relationship between stage and age in a stage-structured population: age distribution and mean age of residence for each stage class, expected remaining life-span for individuals in each stage class, and total life-span conditional on reaching a given stage class.

We illustrate the use of our methods to address specific ecological questions by applying them to several previously published demographic data sets. These questions include: (1) what are the demographic effects of crowding on the tropical palm *Astrocaryum mexicanum*?; (2) how important is the initial rosette size in determining life history of teasel, *Dipsacus sylvestris*?; and (3) how old are reproducing adults in a stage-classified population of pink lady's-slipper, *Cypripedium acaule*? Our results may also be useful for evaluating the adequacy of a given stage-transition model.

Key words: age at first reproduction; age distribution; age- vs. stage-structured populations; Astrocaryum mexicanum; *clonal reproduction;* Cypripedium acaule; *demography;* Dipsacus sylvestris; *Lefkovitch matrices; life history; maternity function; population dynamics; population projection matrices; stage-structured models; survivorship function.*

INTRODUCTION

Stage-classified matrix models of population dynamics are frequently used by ecologists to analyze the demography of species (both plant and animal) in which individual survival, growth, and reproduction are not directly linked to age (e.g., Werner and Caswell 1977, Bierzychudek 1982, Cochran 1986, Harvell et al. 1990; for a review see Caswell 1989), or in which the age of individuals is difficult to determine (e.g., Hughes and Jackson 1980, Hughes 1984, Crouse et al. 1987, Huenneke and Marks 1987, Manly 1990). Many of the demographic measures used, such as population growth rate, reproductive value, and the stable (asymptotic) distribution of individuals between classes, originally were derived within the context of age-structured population models. However, methods for analyzing the implications of a population's stage-transition matrix have been limited in comparison to methods available for life-table analysis. Consequently, few studies of stage-structured populations have gone beyond calculating the stable stage distribution, the stage-specific reproductive value, the population growth rate λ, and associated properties such as the sensitivity and elasticity of λ to changes in the transition probabilities (for a review see Caswell 1986).

Nevertheless, stage-structured demography is based

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on following the survival and growth of individuals from one census time to another, so time—and hence age—are implicit in stage-structured models. Thus, age-based life history traits (e.g., expected total life-span, age at first reproduction, and net reproductive rate) and age-based measures of population dynamics (e.g., the average age of individuals in a stage, stable age distribution, and generation time) are also important attributes of stage-structured populations. Even in those stage-structured populations where age is a poor predictor of future behavior, age distributions capture significant additional information about the timing and duration of critical life history events such as maturation, reproduction, and death.

In this paper we present simple formulas for calculating these and other age-based parameters for stage-structured populations described by the standard transition matrix model. We give formulas for the survivorship function, l_x, and the maternity function, f_x, for general stage-structured populations, which may include multiple types of newborns and clonal growth. These functions generate the complete age-based life table for newborns and all parameters derived from it. In addition, we derive the entire probability distribution of many life history parameters that vary between individuals. Age distributions, and the statistics derived from them, summarize the demographic structure of a population and are easy to interpret. Computing them permits the comparison of age- and stage-structured models and provides a common set of demographic parameters for comparing age- and stage-structured populations and comparing populations with different stage structures.

Caswell (1989) has shown that the net reproductive rate (R_0) and various measures of generation time can be obtained from a stage-structured model using z-transform methods from electrical engineering (see Caswell 1989: Chapter 5 for a description of this method). Caswell's (1989) procedure is straightforward in principle, but the calculations are quite lengthy if the transition matrix is highly connected (containing many non-zero entries). Our formulas require only the dominant eigenvalue of the stage-transition matrix, its associated right and left eigenvectors, and the process of matrix inversion. Reliable software for these operations is widely available (e.g., EISPACK [Applied Mathematics Division, Argonne National Laboratories, Argonne, Illinois, USA], MATLAB [The MathWorks, Natick, Massachusetts, USA], GAUSS [Aptech Systems, Kent, Washington, USA]).

Naturally, all our results rest on an assumption that the underlying stage-transition model is valid for the population being studied. For the results presented here, an essential aspect of the stage-transition model is the assumption that individuals within a stage class are identical with respect to their future fate. If the validity of a stage-transition model is in doubt (and like any model, it is unlikely to be exactly accurate), our results may provide new ways of testing the model's adequacy for the purposes at hand. For example, if it is possible to age a subsample of the population, observed age distributions and the age distributions predicted from the stage-structured model can be compared. Or if a subsample can be followed throughout their lives, the individual life history parameters can be compared with those derived from the stage-structured model. Used in this way, our results generate new predictions, which can be used to test model validity. Wide discrepancies, especially between observed and predicted variances of these parameters, would indicate problems with the adequacy of the chosen set of stage classes as a complete description of an individual's current state and future prospects. Furthermore, our results can be used to generate hypotheses about changes in life history parameters that would result from changes in stage-specific vital rates due to different management policies, changes in the environment, or evolution.

To illustrate the additional information that can be extracted from stage-structured models using our results, we present new analyses of several stage-structured populations based on published studies. However, these are not intended to be complete re-analyses of those populations' demography. We use our results for:

1) Integrative life history summaries that can be interpreted and related to population dynamics, for comparisons between populations. Such comparisons may be useful for evaluating the effects of experimental manipulations (either for hypothesis testing or for improvement of management strategies), or for summarizing demographic changes along environmental gradients or differences between habitat patches.

2) Estimating the time required for the re-establishment of a population of mature individuals.

3) Comparing the life histories of types of newborns (e.g., differences in the life histories of sexual vs. clonal newborns).

THE MODEL

We consider a population described by the standard stage-structured transition model, $\boldsymbol{X}(t+1) = \boldsymbol{A}\boldsymbol{X}(t)$, where $\boldsymbol{X}(t)$ is an n-dimensional population vector with entries $X_j(t)$ = the number of individuals in stage j at time t, and $\boldsymbol{A}$ is an $n \times n$ matrix with entries $A(i, j)$ = average per capita contribution of stage j at time $t - 1$ to stage i at time t. As usual in this model, we ignore demographic stochasticity, i.e., deviations from model projections due to finite population size.

In the following, we let $M(i, j)$ denote the i,j^{th} entry of the matrix $\boldsymbol{M}$; $\boldsymbol{I}$ denotes the identity matrix; and $\boldsymbol{0}$ is the matrix with all entries equal to 0. For a square matrix $\boldsymbol{M}$ and integer k, $\boldsymbol{M}^k$ is $\boldsymbol{M}$ multiplied by itself k times (e.g., $\boldsymbol{M}^3 = \boldsymbol{M}\cdot\boldsymbol{M}\cdot\boldsymbol{M}$), except that $\boldsymbol{M}^0 = \boldsymbol{I}$, $\boldsymbol{M}^{-1}$ is the inverse of $\boldsymbol{M}$ (assuming $\boldsymbol{M}$ is invertible), and

$\mathbf{M}^{-k} = (\mathbf{M}^{-1})^k$. $M^k(i, j)$ denotes the i, j^{th} entry of the matrix $\mathbf{M}^k$. A matrix is called *convergent* if all of its eigenvalues are <1 in magnitude (Isaacson and Keller 1966); this implies that $\mathbf{M}^t \to \mathbf{0}$ as $t \to \infty$. For a vector $\mathbf{u}$, u_j denotes the j^{th} entry of $\mathbf{u}$.

In stage-structured matrix models the matrix $\mathbf{A}$ may contain up to three types of entries. These are: (1) births, represented by $B(i, j)$ = expected value [number of newborns contributed to stage i at time t by an individual in stage j at time $t - 1$]; (2) fission, in which individuals split to form two or more individuals, represented by $F(i, j)$ = E[number of individuals contributed via fission to stage i at time t by individuals in stage j at time $t - 1$]; and (3) survival and growth (or, more acurately, all transfers among stages by surviving individuals, which may involve changes in size or other attributes used to define stage classes), represented by $P(i, j) = \Pr\{$individual is in stage i at time t given that individual is in stage j at time $t - 1\}$. We will refer to $\mathbf{B}$, $\mathbf{F}$, and $\mathbf{P}$ as the "birth," "fission," and "survival" matrices, respectively. These processes implicitly define the age of individuals. Newborns are assigned age 1 at the first census following their birth (see Fig. 1). Individuals of age x at time t become age $x + 1$ at time $t + 1$. Clonal reproduction may be placed in either $\mathbf{F}$ or $\mathbf{B}$, depending on the age one assigns to the "offspring." Clonal offspring in $\mathbf{B}$ are regarded as newborns (age 1). Clonal offspring in $\mathbf{F}$ are regarded as survival of the parent in multiple copies and are the same age as their "parent." Note that the age of offspring in $\mathbf{F}$ is not a parameter that must be measured but a logical consequence of the decision to treat them as a continuation of the parent. In most organisms that reproduce clonally, there is a marked size difference between "parent" and "offspring." Small clonal individuals may be more similar to sexually produced offspring than to mature adults, and therefore should be placed in $\mathbf{B}$ rather than in $\mathbf{F}$. Clonal reproduction without such size asymmetries (e.g., some herbaceous perennials [Cochran 1986]) or the physical division of an individual or colony into viable pieces by an outside agent (e.g., corals [Hughes 1984]) would typically be assigned to $\mathbf{F}$ rather than to $\mathbf{B}$.

Our results are based on the decomposition of the transition matrix $\mathbf{A}$ corresponding to the three types of entries: $\mathbf{A} = \mathbf{B} + \mathbf{F} + \mathbf{P} = \mathbf{B} + \mathbf{C}$, where $C(i, j) = F(i, j) + P(i, j)$. For an individual in stage j at time t, $P^k(i, j)$ is the probability that the individual is alive and in stage i at time $t + k$. For a newborn (whose age at time t is 1), "time $t + k$" is equivalent to "age k + 1." Thus, the matrices $\mathbf{P}$, $\mathbf{P}^2$, $\mathbf{P}^3$, ... summarize the probability of possible fates for a newborn, and the ages at which each event occurs. Consequently, it is possible to express age-specific vital rates (such as l_x) in terms of $\mathbf{P}^k$, and age-based life history parameters (such as R_0) as infinite sums of the $\mathbf{P}^k$s by applying the theory of finite Markov chains (Kemeny and Snell 1976). If clonal reproduction occurs, ($\mathbf{F} \neq \mathbf{0}$), $\mathbf{C}$ must be used instead of $\mathbf{P}$ to account for survival of the individual in multiple copies. If $\mathbf{F} \neq \mathbf{0}$ the entries of $\mathbf{C}$ are a combination of the contribution by fission and the probabilities of survival, rather than genuine transition probabilities.

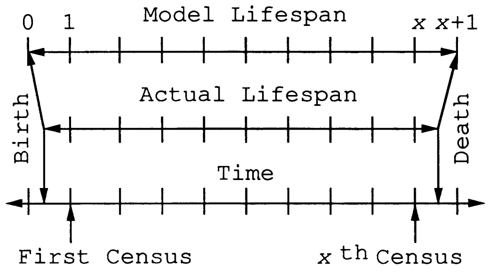

FIG. 1. Model age vs. actual age. Newborns are assigned age 1. In computing individual life-spans, individuals alive at time t but not at time $t + 1$ are treated as if death occurred at time $t + 1$.

To simplify the presentation, we make the following assumptions about the survival and birth matrices: (1) The transition matrix $\mathbf{A}$ has a dominant eigenvalue λ and associated right eigenvector $\mathbf{w}$ and left eigenvector $\mathbf{v}$. λ is then the asymptotic growth rate of the population, $\mathbf{w}$ is the asymptotic or "stable" stage distribution (proportion of individuals in each stage), and $\mathbf{v}$ is the reproductive value (relative contribution of individuals in each stage to future population growth). (For conditions implying the existence of a unique dominant eigenvalue, see Caswell 1989.) (2) At stable stage distribution some individuals are born with positive reproductive value, i.e.,

$$\sum_{i,j=1}^{n} B(i, j)v_i w_j > 0. \qquad (1)$$

(3) $\mathbf{C}$ is convergent, i.e., without any births the population would shrink to extinction. When fission does not occur ($\mathbf{F} = \mathbf{0}$), assuming that $\mathbf{C}$ is convergent is equivalent to the biologically reasonable assumption that each individual eventually dies. However, when fission is included (i.e., $\mathbf{F} \neq \mathbf{0}$), the model is following the dynamics of genets, so defining "death," and thus "lifetime" may be difficult due to the ambiguity of what constitutes an "individual" in a clonal organism. If all ramets in a genet are considered part of a single individual, it is logically possible for genets to be immortal, even though each ramet dies. In such cases, $\mathbf{C}$ need not be convergent. Consequently, it is possible that the $\mathbf{C}$ matrix derived for a successful clonal organism might not be convergent, but most populations can be expected to satisfy the assumption of convergence.

These assumptions are weaker than those needed for Caswell's (1989) derivation of expressions for R_0 and the generation time for stage-structured matrix models. (The precise assumptions required by Caswell [1989] are discussed in Appendix 1.) In particular, our results apply also to models with several types of newborns, e.g., sexual vs. vegetative reproduction, or several stage classes of seedlings, as in teasel (Werner and Caswell 1977, Caswell 1989: section 4.2).

Variable names are summarized in Table 1.

LIFE HISTORY TRAITS

In this section we derive formulas for a number of life history traits: the discrete survivorship function, P_x; the expected remaining life-span of an individual in stage i; the total life-span conditional on reaching stage i; the mean age at maturity; the discrete maternity function, f_x; and the net reproductive rate, R_0. With the exception of the expected remaining life-span of an individual in stage i, all of these measures can be expected to differ for the different newborn types. None of the measures depends upon a stable stage distribution. For measures of individual life-span, we restrict ourselves to populations without fission (i.e., $\boldsymbol{F} = \boldsymbol{0}$) so that "individual" and "life-span" are well defined.

Survivorship function, l_x

Assume first that $\boldsymbol{F} = \boldsymbol{0}$, i.e., any clonal offspring are regarded as newborns rather than as survival of the parent. Then the matrix $\boldsymbol{P}^{x-1}$ represents survival probabilities over an interval of $x - 1$ time units. Let newborns in stage j be called type-j newborns. Then, in particular, for a type-j newborn, $P^{x-1}(i, j)$ is the probability of being alive and in stage class i at age x. Consequently, the probability of survival to age x for a type-j newborn is

$$l_x(j) = \sum_{i=1}^{n} P^{x-1}(i, j), \quad x = 1, 2, \ldots . \qquad (2)$$

Since the age of newborns is known, l_x is a useful measure of comparison between newborns of different types or newborns in different populations.

A more general cohort-based definition of l_x is valid for populations with or without fission. Consider a cohort of type-j newborns. After $x - 1$ time units, the expected fraction of survivors, all aged x, is

$$l_x(j) = \sum_{i=1}^{n} C^{x-1}(i, j), \quad x = 1, 2, \ldots . \qquad (2a)$$

Note that Eq. 2a reduces to Eq. 2 if $\boldsymbol{F} = \boldsymbol{0}$, but if fission occurs, Eq. 2a includes the increases in cohort size due to fission as well as the decreases in cohort size due to mortality. Consequently, if $\boldsymbol{F} \neq \boldsymbol{0}$, the $l_x(j)$ calculated from Eq. 2a cannot be interpreted as a survival probability. While l_x is still the "fraction of survivors" to age x, if fission is very frequent then that fraction may be an increasing function of age x, and may even be >1.

TABLE 1. Definitions of symbols for variables used in this paper.

$\boldsymbol{A}$	Transition matrix, $\boldsymbol{B} + \boldsymbol{P} + \boldsymbol{F}$
$\bar{A}$	Mean age of parents of offspring produced at stable stage distribution, Eq. 26
$\boldsymbol{B}$	Birth matrix
b_j	Distribution of newborns at stable state distribution, Eq. 19
$\hat{b}_j$	Actual distribution of newborns at time t, Eq. 20
b_j^*	Projected distribution of newborns at time t, Eq. 21
$\boldsymbol{C}$	Survivorship and growth matrix + fission matrix, $\boldsymbol{P} + \boldsymbol{F}$
$\boldsymbol{D}_i$	Transition matrix for mean time to first passage to stage i, Eq. 8
$\mathrm{E}[X]$	Expectation (arithmetic mean) of the random variable X
$\boldsymbol{F}$	Fission matrix
f_x	Maternity function, Eq. 13 and Table 2
$\boldsymbol{I}$	The identity matrix
K	The set of reproductive stage classes
L	Expected number of years until death, Eq. 3 and Table 2
l_x	Survivorship function, Eq. 2 and Table 2
$\boldsymbol{P}$	Survivorship and growth matrix
$p_{i,a}$	Fraction of age a individuals in stage i, Eq. 22
$\Pr\{Z\}$	Probability of event Z occurring
$\boldsymbol{Q}$	Transition matrix for age at maturity, Eq. 14
R_0	Net reproductive rate, Eq. 18 and Table 2
S_i	Mean age of residence in state i for the population, Eq. 29 and Table 2
T	Generation time
$\boldsymbol{v}$	Reproductive value, the left eigenvector of $\boldsymbol{A}$
V_x/V_1	Age-specific reproductive value, Eqs. 32 and 33
$\boldsymbol{w}$	Stable stage distribution, the right eigenvector of $\boldsymbol{A}$
$\boldsymbol{X}(t)$	Population vector at time t
Y_i	Age of an individual in stage class i
y_i	Average age in stage class i, Eq. 23
$\boldsymbol{z}$	Dominant right eigenvector of $\boldsymbol{C}$
α_j	Age at maturity for a type-j newborn
β_i	Fecundity of individuals in stage class i, Eq. 11
γ_i	Fecundity of individuals in stage class i in terms of "newborn equivalents," Eq. 12
$\phi(j)$	The set of stage classes which are reachable from class j
Λ_{ij}	Total life-span of type-j newborns, conditional on passing through stage i, Eq. 6
Λ_i	Total life-span of a cohort of newborns, conditional on passing through stage i, Table 2
λ	Population growth rate, dominant eigenvalue of $\boldsymbol{A}$
μ_1	Mean age at which members of a cohort produce offspring, Eq. 27 and Table 2
$\theta(t)$	Fraction of the total offspring born to a cohort at age t
$\psi_i(t)$	Frequency distribution of ages (t) when in stage class i
τ_{ij}	Age when first reaching stage class i from stage class j
ζ	Dominant eigenvalue of $\boldsymbol{C}$
Ω	Remaining life-span
ω	Stable age distribution, Eq. 31

Remaining life-span

Although some organisms with size- or stage-dependent population dynamics may progress directionally through a series of classes, either remaining in the same class or growing into a larger class (e.g., turtles [Crouse et al. 1987], trees [Hartshorn 1975], and some herbaceous perennials [Werner and Caswell 1977]), others may shrink between time periods (e.g., bryozoans [Harvell et al. 1990], corals [Hughes 1984], and other herbaceous perennials [Bierzychudek 1982, Cochran 1986]). In the second case, the survivorship curve for newborns provides no information relating survivorship to current stage: l_x predicts future survivorship only when the current age is known. A more informative measure of future survivorship is $L(j)$, the mean number of time units until death for an individual currently in stage j, i.e., $L(j) =$ E[time until death, given that individual is now in stage j].

Note that in our conventions (as shown in Fig. 1) the death of an individual is recorded when it first fails to appear in a census. Thus, what we are calling "age at death" is actually the "age when not censused again." Similarly, the birth of an individual is retroactively recorded as if it occurred one time step prior to the first census in which the individual appeared. These conventions slightly overestimate age and life-span, with a maximum error of two time steps (when birth occurs immediately prior to the first census and death occurs immediately after the last census). In systems where the timing of birth and death relative to censusing is known to differ from these conventions, appropriate adjustments can be made to all measures of age (e.g., subtract 1 from all ages if birth occurs immediately prior to censusing).

For an individual currently in stage j, let Ω_j be the (random) number of time units until death. We assume that $\boldsymbol{F} = \boldsymbol{0}$, i.e., any clonal offspring are regarded as new individuals rather than as survival of the parent. Thus, the expected number of time units until death is

$$L(j) = E[\Omega_j] = \sum_{t=0}^{\infty} \Pr\{\Omega_j > t\} = \sum_{t=0}^{\infty} \sum_{i=1}^{n} P^t(i, j).$$

Since $\boldsymbol{P}$ is convergent, Eq. 2.1 from Appendix 2 may be applied to yield

$$L(j) = \sum_{i=1}^{n} (\boldsymbol{I} - \boldsymbol{P})^{-1}(i, j). \tag{3}$$

The variance of the remaining life-span may also be computed from the distribution of Ω_j, which is:

$$\begin{aligned}\Pr\{\Omega_j = t + 1\} &= \Pr\{\Omega_j > t\} - \Pr\{\Omega_j > t + 1\}\\ &= \sum_{i=1}^{n} P^t(i, j) - P^{t+1}(i, j)\\ &= \sum_{i=1}^{n} [P^t(I - P)](i, j).\end{aligned} \tag{4}$$

Thus,

$$\begin{aligned}\mathrm{Var}[\Omega_j] &= \mathrm{E}[\Omega_j^2] - (\mathrm{E}[\Omega_j])^2\\ &= \left[\sum_{t=0}^{\infty} (t + 1)^2 \Pr\{\Omega_j = t + 1\}\right] - [L(j)]^2\\ &= \left[\sum_{t=0}^{\infty} (t + 1)^2 \sum_{i=1}^{n} [P^t(I - P)](i, j)\right] - [L(j)]^2.\end{aligned}$$

Using Eq. 2.3 from Appendix 2, this simplifies to

$$\mathrm{Var}[\Omega_j] = \left[\sum_{i=1}^{n} [(I + P)(I - P)^{-2}](i, j)\right] - [L(j)]^2. \tag{5}$$

Conditional total life-span

In organisms with high juvenile mortality, the expected remaining life-span for newborns may be very short; nevertheless, the life-spans of the surviving adults may be long. Since it is the reproductive individuals who ultimately determine the dynamics of a population, it may be more meaningful to determine the average life-span of those individuals that survive to reach some critical developmental stage. In this section we develop a method to determine the mean age at death, conditional on reaching a given stage, which gives a stage-specific measure of total life-span (the *conditional total life-span*). As in the previous section, we assume $\boldsymbol{F} = \boldsymbol{0}$.

For any newborn in class j that reaches stage i, let τ_{ij} be the (random) age at which that individual first reaches stage class i. Thus the life-span of any such newborn can be partitioned into two segments: from birth to age τ_{ij} and from age τ_{ij} to death. Since these two segments are independent, the age at death for a newborn type j that survives to reach stage i has the same probability distribution as $\tau_{ij} + \Omega_i$. Hence, the average age at death for newborns of type j, conditional on passing through stage i at least once, is

$$\Lambda_{ij} = \mathrm{E}(\tau_{ij} + \Omega_i) = \mathrm{E}(\tau_{ij}) + \mathrm{E}(\Omega_i) = \mathrm{E}(\tau_{ij}) + L(i), \tag{6}$$

with variance

$$\mathrm{Var}(\tau_{ij} + \Omega_i) = \mathrm{Var}(\tau_{ij}) + \mathrm{Var}(\Omega_i). \tag{7}$$

To compute the mean and variance of τ_{ij}, we create a new transition matrix $\boldsymbol{D}_i$, so that individuals entering class i spend one time-unit in that class and then die. (This ensures that no individuals will enter stage i more than once, without changing the time required for individuals to reach stage i.) This results in the matrix $\boldsymbol{D}_i$, where

$$D_i(k, l) = \begin{cases} P(k, l), & l \neq i \\ 0 & l = i. \end{cases} \tag{8}$$

Thus, for type-j newborns, the probability of first reaching stage i after $t + 1$ time units is $D_i^t(i, j)$ and $\sum_{t=0}^{\infty} D_i^t(i, j)$ is the probability of reaching stage i before dying. Thus, for those type-j newborns that ever reach stage i, the probability of doing so after $(t + 1)$ time units is

$$\frac{D_i^t(i, j)}{\sum_{s=0}^{\infty} D_i^s(i, j)}.$$

Since $D_i(k, l) \leq P(k, l)$, $D_i^t(k, l) \leq P^t(k, l)$; therefore, since $\boldsymbol{P}$ is convergent, the matrix $\boldsymbol{D}_i$ is convergent also.

Thus, using Eqs. 2.1 and 2.2 from Appendix 2, for those individuals that ever reach stage i, the mean time to first reach stage i from stage j is

$$\mathrm{E}(\tau_{ij}) = \frac{\sum_{t=0}^{\infty} (t+1) D_i^t(i, j)}{\sum_{t=0}^{\infty} D_i^t(i, j)} = \frac{(I - D_i)^{-2}(i, j)}{(I - D_i)^{-1}(i, j)}. \quad (9)$$

Applying Eq. 2.3 from Appendix 2, the variance of time to first reach stage i from stage j, conditional on reaching stage i is

$$\mathrm{Var}(\tau_{ij}) = \frac{\sum_{t=0}^{\infty} (t+1)^2 D_i^t(i, j)}{\sum_{t=0}^{\infty} D_i^t(i, j)} - [\mathrm{E}(\tau_{ij})]^2$$

$$= \frac{(I + D_i)(I - D_i)^{-3}(i, j)}{(I - D_i)^{-1}(i, j)} - [\mathrm{E}(\tau_{ij})]^2. \quad (10)$$

Maternity function, f_x

For discrete-time demographic models based on age, such as the Leslie matrix or discrete life table, the most general summary parameter for age-specific fecundity is f_x (sometimes called F_x). f_x is defined to be the average number of newborns in the population at time $t + 1$, produced by an individual age x at time t. Note that f_x incorporates any mortality of individuals alive at time t prior to reproduction, and does not count offspring that die before time $t + 1$. Consequently, the relationship between f_x and the continuous-time maternity function m_x depends upon the timing of reproduction relative to the census times t and $t + 1$ (Caswell 1989).

In populations with multiple types of newborns, two complications arise in defining f_x. First, newborns of different types may have very different life histories, so, as with l_x, we must define a stage-specific maternity function, $f_x(j)$, for each newborn type, j. Secondly, as Caswell (1985) noted, merely counting offspring does not completely describe an individual's fecundity. For an individual in stage class i, the average total number of offspring including all modes of reproduction is

$$\beta_i = \sum_{j=1}^{n} B(j, i). \quad (11)$$

This gives equal weight to all types of offspring, but when there are multiple types of newborns, the relative contribution of the various types of offspring to the future growth of the population is expected to differ. These differences in the newborns' contribution to future generations are summarized by their reproductive value, v_j (Caswell 1985). Thus, offspring of differing types can be expressed in a common currency by measuring the total reproductive value of all offspring, which we will call "newborn equivalents." The number of newborn equivalents produced on average by an individual in stage class i is

$$\gamma_i = \sum_{j=1}^{n} B(j, i)\frac{v_j}{v_k}, \quad (12)$$

where k is a reference newborn stage to which all newborn types are compared (e.g., seeds in plants). Thus, γ_i is the fecundity of individuals in stage class i, including all modes of reproduction, weighted to account for the relative reproductive value of different types of offspring. When there is only one newborn type (say, stage class k), Eq. 12 reduces to $\gamma_i = \beta_i = B(k, i)$.

To compute f_x, consider a cohort of newborns in stage class j at time 0. After $x - 1$ time units their age is x and their expected frequency distribution over stages (including mortality and fission) is

$$\frac{C^{x-1}(i, j)}{\sum_{k=1}^{n} C^{x-1}(k, j)}, \qquad i = 1, 2, \ldots, n.$$

Consequently, their effective total offspring production (in newborn equivalents per individual) is

$$f_x(j) = \frac{\sum_{i=1}^{n} C^{x-1}(i, j)\gamma_i}{\sum_{i=1}^{n} C^{x-1}(i, j)}, \qquad x = 1, 2, \ldots. \quad (13)$$

If fission does not occur ($\boldsymbol{F} = \boldsymbol{0}$), then $\boldsymbol{C} = \boldsymbol{P}$ and Eq. 13 reduces to the standard definition of f_x for age-based models: it gives the expected number of offspring at age x, conditional on surviving to age x.

Age at first reproduction

In age-based models, the "age at first reproduction" is the minimum age at which individuals first reproduce, i.e., it is the age at which individuals first enter a class in which *some* individuals are reproducing. There are two possible ways of extending this concept to stage-transition models. The first is to locate the shortest path from a given newborn stage to a stage with positive fecundity. The second is to calculate an average age (over all newborns) at which an individual enters a stage class that has positive fecundity. In age-based models these are identical, but in a stage-transition model there are important differences. In most cases very few individuals will follow the shortest possible path. Thus the first measure is describing atypical life histories. Indeed, the shortest path in the model may be an artifact of the assumption that all individuals in a stage class are identical, and no single individual in the population could achieve all the necessary transitions in successive time steps.

We therefore suggest that the second definition, which we call "mean age at maturity," is the preferable analog to the standard "age at first reproduction." Averaging over a cohort of newborns eliminates the focus on atypical and possibly artifactual life histories, giving a summary value that is more representative of the population and more robust to deviations from model assumptions. Also, the mean age at maturity does not depend on the population structure and can be calculated without the assumption of stable stage distribution. However, if there are multiple modes of reproduction, the mean age at maturity may vary among the different types of newborns in the population (i.e., sexual vs. vegetative in plants).

Let α_j denote the (random) age at maturity for type-j newborns that reach maturity before dying. To compute the distribution of α_j we proceed as we did above to compute the conditional life-span: modify the transition matrix so that individuals entering a reproductive class spend one time unit in that class and then die. This has no effect on maturation times for individuals that mature, but ensures that individuals appear in a reproductive class only at their time of maturation. Formally, let K be the set of reproductive classes, $K = \{k = 1, \ldots, n \mid \beta_k > 0\}$. The modified transition matrix is $\boldsymbol{Q}$, where

$$Q(i, j) = \begin{cases} P(i, j), & j \notin K, \\ 0, & j \in K. \end{cases} \qquad (14)$$

Summing the probabilities of entry into each reproductive class and repeating the arguments used to derive Eq. 9, we have

$$\mathrm{E}(\alpha_j) = \frac{\sum_{i \in K} (I - Q)^{-2}(i, j)}{\sum_{i \in K} (I - Q)^{-1}(i, j)}. \qquad (15)$$

Applying Eq. 2.3 from Appendix 2, the variance of the age at maturity for individuals born into class j conditional on reaching maturity is

$$\begin{aligned} \mathrm{Var}(\alpha_j) &= \frac{\sum_{t=0}^{\infty} \sum_{i \in K} (t + 1)^2 Q^t(i, j)}{\sum_{t=0}^{\infty} \sum_{i \in K} Q^t(i, j)} - [\mathrm{E}(\alpha_j)]^2 \\ &= \frac{\sum_{i \in K} \{[I + Q][I - Q]^{-3}\}(i, j)}{\sum_{i \in K} (I - Q)^{-1}(i, j)} - [\mathrm{E}(\alpha_j)]^2. \qquad (16) \end{aligned}$$

As with l_x, for populations with fission it is necessary to adopt a cohort-based definition for the mean age at maturity. Recall that the age of a clone is the time elapsed since its initial member appeared as a newborn. If $\boldsymbol{Q}$ is defined with $\boldsymbol{C}$ in place of $\boldsymbol{P}$, Eq. 15 and 16 give the mean and variance of the cohort's frequency distribution of times of first entry into a reproductive class. For individuals that undergo fission prior to reaching a reproductive class for the first time, the age at maturity of each clone will be included in the calculation, while fission that occurs after maturity is not included.

The greater robustness of "mean age at maturity" and its use in examining a model's adequacy are illustrated by the stage-transition model for loggerhead turtles presented by Crouse et al. (1987). The age at first reproduction is estimated to be 22 yr (Frazer 1983), whereas in Crouse et al.'s model the age at first reproduction (defined in terms of the shortest path to a reproductive class) is 5 yr. This indicates that Crouse et al.'s model, if taken as a description of individual life histories, includes biologically unreasonable life histories. The mean age at maturity for this model is ≈12 yr. This measure is affected, but not completely dominated, by the model's omission of the actual constraints on life histories, and is therefore more accurate. However, in species such as loggerheads in which reproduction is closely tied to age, the mean age at maturity estimated from a stage-transition model should be interpreted with caution. Crouse et al.'s (1987) stage classification was adapted specifically to the availability of data and to address particular management options. Its errors in predicting the age dependence of fecundity in the population indicate that this model should not be used for examining individual life histories, or life history evolution, in loggerheads.

Net reproductive rate

In age-based demography, the net reproductive rate, R_0, is the average number of offspring produced by an individual over its life-span. To allow for populations with multiple newborn types, we need to define R_0 in terms of γ_i, fecundity weighted by the relative reproductive value of newborn types. For type-j newborns, the effective net reproductive rate is

$$R_0(j) = \sum_{t=0}^{\infty} \sum_{i=1}^{n} C^t(i, j)\gamma_i = \sum_{i=1}^{n} (I - C)^{-1}(i, j)\gamma_i. \qquad (17)$$

Eq. 17 is, in fact, identical to the standard age-based definition of R_0, since it is easy to show (using Eqs. 2a, 13 and 2.1) that

$$R_0(j) = \sum_{x=1}^{\infty} l_x(j) f_x(j). \qquad (18)$$

When there is only one newborn type, Eq. 17 gives the average number of offspring produced by an individual in its lifetime. Note that using β_i instead of γ_i in Eq. 17 gives $R_0(j)$ in terms of the total number of offspring, without any weighting for relative offspring quality.

POPULATION AVERAGES OF LIFE HISTORY TRAITS

To accommodate populations with multiple types of newborns, we have derived the life history parameters for each type separately. However, for comparisons between populations or between species, it may be preferable to use average life history parameters for each population. These parameters are the topic of this section. If there is only one type of newborn, they reduce to the parameter value for that type. If there are several

TABLE 2. Population life history parameters (defined in Table 1) weighted for each class of newborns. Formulas for the variances of conditional total life-span and α are derived in Appendix 4.

$$l_x = \sum_{j=1}^{n} l_x(j)b_j, \qquad x = 1, 2, \ldots$$

$$f_x = \sum_{j=1}^{n} f_x(j)b_j, \qquad x = 1, 2$$

$$R_0 = \sum_{j=1}^{n} R_0(j)b_j,$$

$$L = \mathrm{E}(\Omega) = \sum_{i=1}^{n} L(j)b_j,$$

$$\mathrm{Var}(\Omega) = \sum_{i=1}^{n}\sum_{j=1}^{n} [(I + P)(I - P)^{-2}](i, j)b_j - L^2.$$

$$\Lambda_i = L(i) + \frac{\sum_{j=1}^{n} (I - D_i)^{-2}(i, j)b_j}{\sum_{k=1}^{n} (I - D_i)^{-1}(i, k)\, b_k},$$

$$\mathrm{E}(\alpha) = \frac{\sum_{j=1}^{n}\sum_{i\in K} (I - Q)^{-2}(i, j)b_j}{\sum_{j=1}^{n}\sum_{i\in K} (I - Q)^{-1}(i, j)b_j}.$$

$$\mu_1 = \mathrm{E}[\theta(t)] = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} (I - C)^{-2}(i, j)\gamma_i b_j}{R_0}.$$

$$\mathrm{Var}[\theta(t)] = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} \{[I-C]^{-3}[I + C]\}(i, j)\gamma_i b_j}{R_0} - (\mu_1)^2.$$

$$S_i = \mathrm{E}[\psi_i(t)] = \frac{\sum_{j=1}^{n}\sum_{t=0}^{\infty} (t + 1)C^t(i, j)b_j}{\sum_{j=1}^{n} (I - C)^{-1}(i, j)b_j}$$

$$= \frac{\sum_{j=1}^{n} (I - C)^{-2}(i, j)b_j}{\sum_{j=1}^{n}(I - C)^{-1}(i, j)b_j}.$$

$$\mathrm{Var}[\psi_i(t)] = \frac{\sum_{j=1}^{n}\sum_{t=0}^{\infty} (t + 1)^2C^t(i, j)b_j}{\sum_{j=1}^{n} (I - C)^{-1}(i, j)b_j} - (S_i)^2$$

$$= \frac{\sum_{j=1}^{n} (I + C)(I - C)^{-3}(i, j)b_j}{\sum_{j=1}^{n} (I - C)^{-1}(i, j)b_j} - (S_i)^2.$$

types of newborns, differences between populations may result from either (a) between-population differences in the life history traits of at least one newborn type, or (b) differences in the relative frequencies of newborn types. The population averages defined here combine these effects into one overall measure for each population.

To compute the population's average life history traits at stable stage distribution, recall that the stable stage distribution of the population is $\boldsymbol{w}$, the right eigenvector of $\boldsymbol{A}$ associated with the dominant eigenvalue, λ. Define

$$b_j = \frac{(\boldsymbol{B}\boldsymbol{w})_j}{\sum_{i=1}^{n} (\boldsymbol{B}\boldsymbol{w})_i}. \tag{19}$$

Thus, the vector $\boldsymbol{b} = (b_1, b_2, \ldots, b_n)$ is the stage frequency of newborns at stable stage distribution, i.e., b_j is the fraction of newborns that are type j. Weighting the life history parameters for each class of newborns by the b_js gives overall life history parameters for the population at stable stage distribution. (Formal derivations of population averages for total life-span conditional on passing through stage class i and the age of maturity are given in Appendix 3.) The formulas for these parameters are shown in Table 2.

The formulas in Table 2 can be applied to populations not at stable stage distribution in two ways that have different biological interpretations:

1) They may be computed directly from the formulas in Table 2. The values obtained can be regarded as estimates for the long-term behavior of the population.

2) A weighted average based on the current state of the population can be computed. If newborns can be identified in the field, the formulas in Table 2 are used with b_j replaced by $\hat{b}_j$, the current stage distribution of newborns,

$$\hat{b}_j = \frac{\text{number of newborns in stage class } j}{\text{total number of newborns in all stage-classes}}. \tag{20}$$

Otherwise, the stage distribution of newborns can be projected from the current population and the birth matrix $\boldsymbol{B}$,

$$b_j^*(t) = \frac{\sum_{k=1}^{n} B(j, k)X_k(t)}{\sum_{i=1}^{n}\sum_{k=1}^{n} B(i, k)X_k(t)}. \tag{21}$$

Using $\hat{\boldsymbol{b}}$ or $\boldsymbol{b}^*$ in place of $\boldsymbol{b}$ in Table 2 gives estimated average life history parameters for the current cohort of newborns in the population.

In the rest of this paper we always use b_j in defining population averages, but in all cases $\hat{b}_j$ or b_j^* can be used instead to get estimates for the current population state.

POPULATION DYNAMICS

In this section we derive formulas for measures associated with population dynamics: the average age of an individual in stage class i; the stable age distribution; age-specific reproductive value; generation time; and "mean time of residence" in stage i. These population measures depend on the distribution of individuals between classes and assume the stable stage distribution has been attained. In addition, the average age of individuals in stage class i may be calculated under nonequilibrium conditions to give an estimate of the rate of convergence to the stable age distribution.

Age composition in stage class i

In this section we derive the asymptotic ($t \to \infty$) distribution of ages among individuals in a given stage class i, i.e., $p_{i,a}$ = fraction of individuals in stage i whose age is a. Given this age distribution, it is then straightforward to calculate the asymptotic mean, variance, median, etc. of the ages of individuals in stage i.

To derive the asymptotic distribution, we use the fact that a model population reaching stable stage distribution remains there indefinitely. Therefore, the asymptotic age distribution corresponds to a population that has been in the stable stage distribution, $\mathbf{w}$, and growing at a rate λ, for an infinite period of time in the past. Let $t = 0$ be the present time. The number of type-j newborns at time $-t$ is proportional to $\lambda^{-t}b_j$. For each of these newborns, $C^t(i, j)$ individuals are in stage i at time 0 and their age is $t + 1$. Summing the inputs from newborns of all stage classes, the total number of age $t + 1$ individuals in stage i at time 0 is proportional to $\lambda^{-t} \Sigma_j C^t(i, j)b_j$. The fraction of age $a + 1$ individuals in stage i is therefore

$$p_{i,a+1} = \frac{\lambda^{-a} \sum_{j=1}^{n} C^a(i, j)b_j}{\sum_{t=0}^{\infty} \left\{\lambda^{-t} \sum_{j=1}^{n} C^t(i, j)b_j\right\}} = \frac{\lambda^{-a} \sum_{j=1}^{n} C^a(i, j)b_j}{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-1}(i, j)b_j}, \qquad (22)$$

using Eq. 2.1 to simplify the denominator since the eigenvalues of $\lambda^{-1}\mathbf{C}$ have magnitude <1 (for a proof, see Appendix 4). Let Y_i be the age of an individual in stage i. The average age in stage i is then

$$y_i = \mathrm{E}[Y_i] = \frac{\sum_{t=0}^{\infty} (t + 1)\lambda^{-t} \sum_{j=1}^{n} C^t(i, j)b_j}{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-1}(i, j)b_j}.$$

The numerator simplifies using Eq. 2.2 from Appendix 2. Thus, the stable average age of individuals in stage i is

$$y_i = \frac{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-2}(i, j)b_j}{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-1}(i, j)b_j}. \qquad (23)$$

By using Eq. 23, the mean ages y_i can be obtained without computing the entire age distribution. Similarly, using Eqs. 22 and 2.3, the variance of the age distribution in stage i reduces to

$$\mathrm{Var}(Y_i) = \frac{\sum_{t=0}^{\infty} \sum_{j=1}^{n} (t + 1)^2[\lambda^{-1}C]^t(i, j)b_j}{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-1}(i, j)b_j} - (y_i)^2$$

$$= \frac{\sum_{j=1}^{n} \{(I + \lambda^{-1}C)(I - \lambda^{-1}C)^{-3}\}(i, j)b_j}{\sum_{j=1}^{n} (I - \lambda^{-1}C)^{-1}\}(i, j)b_j} - (y_i)^2. \qquad (24)$$

For populations that have not reached stable stage distribution, an alternate method can be used to project transient changes over time in the mean age of individuals in each stage class. Let $y_i(t)$ be the average age of individuals in stage class i at time t. An individual arrives in stage i at time $t + 1$ in one of three ways:

1) by remaining in stage i from time t to time $t + 1$; the average age of these individuals at time $t + 1$ is $1 + y_i(t)$;

2) by moving from stage j at time t to stage i at time $t + 1$; the average age of these individuals at time $t + 1$ is $1 + y_j(t)$ for each j, $j \neq i$; or

3) by being born into stage i at time $t + 1$; all of these individuals are age 1.

Weighting these by the number of individuals following each route into stage i gives

$$y_i(t + 1) = \frac{\sum_{j=1}^{n} [1 + y_j(t)]C(i, j)X_j(t) + \sum_{j=1}^{n} B(i, j)X_j(t)}{X_i(t + 1)}. \qquad (25)$$

Thus, if the population's age composition is known at a particular time (i.e., it has been followed since establishment or long enough that the "birthdate" of each individual is known), the age composition can be projected into the future. In addition, Eq. 25 can be used to determine the time required for convergence to the asymptotic mean age in each stage, by choosing a variety of initial age compositions and projecting ahead.

The formulas above have tacitly assumed that all stages are represented at the stable stage distribution (i.e., all $w_i > 0$). This will generally be true, unless the population actually consists of two or more sub-populations without mutual exchange of individuals. However, if some $w_i = 0$, the asymptotic age distributions for all stages can still be found, by the methods presented in Appendix 5.

Generation time

Generation time is an important parameter for both empirical and theoretical studies. One generation is a minimal duration for long-term demographic studies. Life histories with identical net reproductive rates but different generation times will have different population growth rates; all else being equal, the type with the shortest generation time will have the highest population growth rate and thus will be favored. Generation time also gives a measure of the potential rate at which evolution can act.

Three measures of generation time have been defined (Coale 1972), and each can be calculated directly from the survival, fission, and birth matrices. The first measure, T, is defined to be the time required for a population at stable stage distribution to grow by the net reproductive rate, R_0. That is, $T = \ln R_0 / \ln \lambda$ (Coale 1972, Caswell 1989). The second measure, $\bar{A}$, is the mean age of the parents of offspring produced in the current time period, once the population has reached stable stage distribution. Thus,

$$\bar{A} = \frac{\sum_{i=1}^{n} y_i w_i \gamma_i}{\sum_{i=1}^{n} w_i \gamma_i}. \qquad (26)$$

The third measure, μ_1, is the mean age at which members of a cohort of newborns produce offspring (i.e., the age of the parents weighted by the number of offspring they produce at each age). Unlike T and $\bar{A}$, μ_1 does not assume a population is at stable stage distribution. For all individuals in a cohort, their total offspring production is tabulated as a function of the parent's age; the histogram of (number of offspring) vs. (age of parent) is scaled to have total area 1, and regarded as a frequency distribution, $\theta_j(t)$, for the age at reproduction. The mean of that distribution is μ_1. For individuals entering the population as newborns in stage class j,

$$\mu_1(j) = \mathrm{E}[\theta_j(t)] = \frac{\sum_{t=0}^{\infty} \sum_{i=1}^{n} (t+1) C^t(i, j) \gamma_i}{R_0(j)}$$

$$= \frac{\sum_{i=1}^{n} (I - C)^{-2}(i, j) \gamma_i}{R_0(j)}. \qquad (27)$$

Our expression for $\mu_1(j)$ is exactly parallel to the definition of μ_1 for age-structured models. The corresponding variance of the distribution for age at reproduction is

$$\mathrm{Var}[\theta_j(j)]$$

$$= \frac{\sum_{t=0}^{\infty} \sum_{i=1}^{n} (t+1)^2 C^t(i, j) \gamma_i}{R_0(j)} - [\mu_1(j)]^2$$

$$= \frac{\sum_{i=1}^{n} \{(I + C)(I - C)^{-3}\}(i, j) \gamma_i}{R_0(j)} - [\mu_1(j)]^2. \qquad (28)$$

The age-at-reproduction distributions for all classes of newborns can be combined into an overall measure for the population (Table 2). As with the maternity function and net reproductive rate, when there are multiple types of newborns, the generation time measures may also be computed based on the raw numbers of offspring, without weighting for relative reproductive value, by substituting β_i for γ_i. In addition, nonequilibrium measures for generation time may be computed by using the nonequilibrium value of R_0 and substituting $\boldsymbol{X}(t)$ for $\boldsymbol{w}$ in Eq. 26.

Mean age of residence

The ideas leading to the definition of μ_1 can be adapted to give another measure of the relationship between "age" and "stage" in a stage-structured population. μ_1 tells when (on average) a cohort of newborns will produce offspring. Similarly, for any stage i, we can ask when (on average) a cohort of newborns will be in that stage. We call this the "mean age of residence," S_i.

Mean age of residence is an important measure of the relationship between age and stage in three particular cases: (1) In contrast with y_i, the mean age of individuals in stage i, the definition of S_i, is not based on an assumption of stable stage distribution. Consequently, the mean age of residence may be more meaningful for short-lived populations that spend a large proportion of their duration far from stable stage distribution. (2) Birth rates do not enter into the calculation of S_i. Because all births of a cohort occur simultaneously, the age of individuals in a cohort does not depend on the rate at which the population is growing or declining. (Birth rates appear in the y_i in the form of the population growth rate, λ.) It is often the case that birth rates show higher temporal variability than survivorships, and values of S_i would be more robust than y_i against this form of departure from the model's assumptions. (3) In populations with λ significantly different from 1, the values of the y_i reflect the population-level consequences of the growth rate. In populations with $\lambda > 1$, relatively more individuals in a stage class were produced in recent cohorts, skewing the y_i towards younger ages; when $\lambda < 1$, the opposite trend occurs. Thus, when comparing two populations with differing growth rates, the S_i are a measure of the differences due to survival and movement between stages, while the y_i summarize the effects of survival, movement between stages, and the birth rate.

For type-j newborns, the probability of being in stage class i at age $(t + 1)$ is $C^t(i, j)$, provided there exists at least one path from stage class j to stage class i (i.e., there exists a t so that $C^t(i, j) > 0$). Denote the set of all such stage classes as $\phi(j)$, i.e., $\phi(j) = \{i = 1, \ldots, n \mid C^t(i, j) > 0 \text{ for some } t \geq 0\}$. For $i \in \phi(j)$, the probability of being in stage class i at age $(t + 1)$ may be rescaled to obtain a probability distribution (or more precisely an expected frequency distribution for the cohort) of ages when in stage i, $\psi_{i,j}(t)$. The mean of this distribution, the "mean age of residence" in stage i, is

$$S_i(j) = \mathrm{E}[\psi_{i,j}(t)] = \frac{\sum_{t=0}^{\infty} (t+1)C^t(i,j)}{\sum_{t=0}^{\infty} C^t(i,j)}$$

$$= \frac{(I-C)^{-2}(i,j)}{(I-C)^{-1}(i,j)}, \qquad \text{for } i \in \phi(j). \tag{29}$$

The variance of this distribution is

$$\mathrm{Var}[\psi_{i,j}(t)] = \frac{\sum_{t=0}^{\infty} (t+1)^2 C^t(i,j)}{(I-C)^{-1}(i,j)} - [S_i(j)]^2$$

$$= \frac{(I+C)(I-C)^{-3}(i,j)}{(I-C)^{-1}(i,j)} - [S_i(j)]^2,$$

$$\text{for } i \in \phi(j). \tag{30}$$

Weighting the expected frequency distributions (for newborns of each type j) of ages when in stage i by the relative contribution of each newborn class generates a distribution for age-of-residence in stage class i for the population. The formulas for the mean and variance of this distribution are shown in Table 2.

Stable age distribution

In the Leslie model of age-structured population dynamics, the stable age distribution has at most n non-zero values, where n is the maximum life-span in the model. However, the standard stage-transition model permits arbitrarily long life-spans if there is looping or cycling between stages. Thus, the stable age distribution may have an infinite number of non-zero terms. Define ω_t as the asymptotic fraction of age t individuals in the population. Thus, ω_t is the weighted average of the age distributions for each stage, i.e., the probability of being age t for individuals in stage class i, times the fraction of the population in stage class i:

$$\omega_t = \frac{\sum_{i=1}^{n} p_{i,t} w_i}{\sum_{i=1}^{n} w_i}, \qquad t = 1, 2, 3, \ldots, \tag{31}$$

where $p_{i,t}$ is given in Eq. 22.

Age-specific reproductive value, $\mathbf{V}_x/\mathbf{V}_1$

In stage-structured populations, the stage-specific reproductive value of individuals, i.e., the extent to which individuals in stage i contribute to future generations, is given by $\boldsymbol{v}$, the left eigenvector of $\boldsymbol{A}$ associated with λ. The most direct approach for determining the age-specific reproductive value (V_x/V_1) is to express it in terms of $\boldsymbol{v}$. Initially, consider a cohort of newborns at stable stage distribution. At birth (age 1) the average reproductive value of the cohort is the weighted average of the stage-specific reproductive value of newborns: $\Sigma_i\, v_i b_i$. By convention, the age-specific reproductive value is scaled so that newborns have reproductive value 1, so we scale v_j so that $\Sigma_j v_j b_j = 1$ (i.e., the average reproductive value of individuals in the cohort at birth is 1). Relative to the cohort, the age-specific reproductive value at birth of type-j newborns is v_j. At later ages, the reproductive value of type-j newborns (relative to the cohort at birth) is

$$\frac{V_x(j)}{V_1} = \frac{\sum_{i=1}^{n} v_i C^{x-1}(i,j)}{\sum_{i=1}^{n} C^{x-1}(i,j)}. \tag{32}$$

A population measure of reproductive value at age x is obtained by averaging over all newborns in the cohort, giving

$$\frac{V_x}{V_1} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} v_i C^{x-1}(i,j) b_j}{\sum_{i=1}^{n}\sum_{j=1}^{n} C^{x-1}(i,j) b_j}. \tag{33}$$

It is also possible (but not as simple) to derive Eqs. 32 and 33 directly from the definition of age-specific reproductive value (Fisher 1930).

In age-structured populations, reproductive value usually tends to 0 as $x \to \infty$. However, in size-structured populations this may not be the case. Just as the maternity function for a cohort of individuals of age x approaches a constant as $x \to \infty$ because the cohort approaches a stable stage distribution, the reproductive value of individuals age x approaches a constant as $x \to \infty$. In particular, if $\boldsymbol{C}$ has a dominant eigenvalue ζ, with associated right eigenvector $\boldsymbol{z}$, scaled so that $\Sigma_i z_i = 1$, it can be shown using standard damping ratio arguments that

$$\lim_{x\to\infty} \frac{V_x(j)}{V_1} = \sum_{i=1}^{n} v_i z_i, \qquad \text{for } j = 1, \ldots, n. \tag{34}$$

APPLICATIONS

To illustrate the usefulness of these measures, we have applied them to three studies in which ecologists used stage-transition models to synthesize demographic data. These examples illustrate the type of ecological questions that can be addressed using our methods. The computer programs that carry out the numerical calculations for specific examples are available as FORTRAN source code on diskette.[2]

How does crowding affect the demography of Astrocaryum mexicanum*?*

Pinero et al. (1984) used a stage-transition model to study the effects of crowding on the demography and population growth of *Astrocaryum mexicanum*, a trop-

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[2] See ESA Supplementary Publication Service Document No. 9202 for 40 pages of supplementary material. This document is available on diskette. For a copy of this document on diskette order from The Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318 USA.

TABLE 3. Stage classes for example matrices: *Astrocaryum mexicanum* (Pinero et al. 1984); *Dipsacus sylvestris* (Caswell 1989, Werner and Caswell 1977); *Cypripedium acaule* (Cochran 1986).

Stage	*Astrocaryum*	*Dipsacus*	*Cypripedium*
1	Fruits	Dead or dormant seeds, yr 1	Seeds
2	Infants	Dead or dormant seeds, yr 2	Corms (yr 1)
3	Juveniles	Small rosettes	Corms (yr 2)
4	Immature	Medium rosettes	Corms (yr 3)
5	Mature 1	Large rosettes	Dormant
6	Mature 2	Flowering plants	1 leaf
7	Mature 3		2 leaves, no flower
8	Mature 4		Flowering plants
9	Mature 5		
10	Mature 6		

ical palm. Two plots at each of three densities were studied from 1975 through 1981 (Pinero et al. 1984). The life cycle of *A. mexicanum,* and the matrices used in our analysis are described in Table 3 and Appendix 6.

With the exception of age at maturity and the maternity function, all life history parameters tend to decrease with increasing density (Table 4, Fig. 2). The differences between plots in the population growth rate, λ, were small, but there were substantial differences in individual life history parameters (Table 4, Fig. 2). In general, individuals growing under low-density conditions had higher survivorship (Fig. 2), longer remaining life-span in the various stage classes, and a higher net reproductive value (Table 4) than individuals in medium- or high-density plots. However, due to the high fecundity of stage-10 adults in the high-density plots, the maternity function f_x increased with density (Fig. 2). These results confirm the conclusions of Pinero et al. (1984) that density is important in determining the life history, and consquently the population dynamics, of *A. mexicanum.* Our analysis also suggests specific biological explanations for the observed differences between treatments. Trees growing in low-density plots have a higher probability of surviving to maturity, even though the age at maturity is older than in medium-density plots, because trees in the early stage classes grow slower in the low-density plots.

As $x \rightarrow \infty$, the logarithm of the survivorship function l_x appears to approach a straight line, while the maternity function appears to approach a constant (Fig. 2). Biologically, this occurs because the cohort is approaching a stable stage distribution, and hence stable birth and mortality rates. Mathematically, this occurs since the $\boldsymbol{C}$ matrices for all three populations are convergent, and each has a single dominant eigenvalue. The stable stage distribution for surviving members of a cohort is then given by the dominant right eigenvector of $\boldsymbol{C}$. The asymptotic birth and mortality rates are the same for all newborn types, because the stable stage distribution is the same for all newborn types in *A. mexicanum.* In general, the asymptotes will be identical whenever all newborn types have a positive probability of entering a stage class that is present in the cohort's stable stage distribution $\boldsymbol{z}$.

Crowding also affected the various measures of generation time for the three populations of *A. mexicanum.* Both T and $\bar{A}$ differed directionally between populations (Table 4): the high-density plots had the longest generation time, followed by medium density, with low-density plots having the shortest generation time. However, μ_1 was virtually indistinguishable between plots. The high variance in μ_1 is mostly due to the long duration of the reproductive phase (roughly from age 25 until death).

What are the lifetime consequences of initial rosette size in teasel, Dipsacus sylvestris*?*

Teasel, *Dipsacus sylvestris,* is a semelparous herbaceous perennial that reproduces totally by seeds. In a stage-classified model of *D. sylvestris,* described in Appendix 6, dormant seeds and the various sizes of 1st-yr rosettes appear as several classes of newborns (Werner and Caswell 1977, Caswell 1989). The effects of

TABLE 4. Selected life history parameters for *Astrocaryum mexicanum* on low-, medium- and high-density plots, based on the data of Pinero et al. (1984). See Table 3 and Appendix 6 for details of the stage-transition matrices.*

	High density	Medium density	Low density
λ	1.007	1.010	1.018
R_0	3.87	5.29	14.61
Pr(maturity)	.0011	.0019	.0039
E(α)	52.8	36.2	43.5
SD(α)	28.2	20.1	24.7
T	197.5	169.2	153.6
$\bar{A}$	152.5	122.8	105.1
μ_1	275.2	261.8	275.5
SD (μ_1)	202.5	201.4	202.3

* Pr(maturity) is a newborn's probability of surviving to enter a stage in which reproduction occurs, and α is the mean age (in years) when this occurs for individuals that survive to maturity.

those size differences on population growth were addressed in Caswell and Werner (1978). Here we extend their analysis by determining the effects of initial size on lifetime net reproductive rates and survivorship.

Since *Dipsacus* is semelparous with only one maternal stage class, the value of R_0 for each newborn type is proportional to the probability of reaching maturity (Table 5). There are noticeable differences in the survivorship function of the various newborn classes (Fig. 3), with the largest (type 5) newborns declining more rapidly because they reach the reproductive stage class (and hence death) more quickly than the other types. Although the smallest (type 1) newborns initially have the highest survivorship ($l_2(1) = 0.994$, $l_3(1) = 0.286$, $l_4(1) = 0.289$, $l_5(1) = 0.917$), after age 3 they have lower survivorship values than either type 3 or type 4. In all types, both the maternity function and the slope of the log-transformed survivorship function rapidly approach their asymptotic values. The difference in $f_x(j)$ between type 5 and the other three types of newborns (Fig. 3) occurs because type-5 newborns can only remain the same size or reproduce while the other newborn types eventually may reproduce either from stage 4 or stage 5.

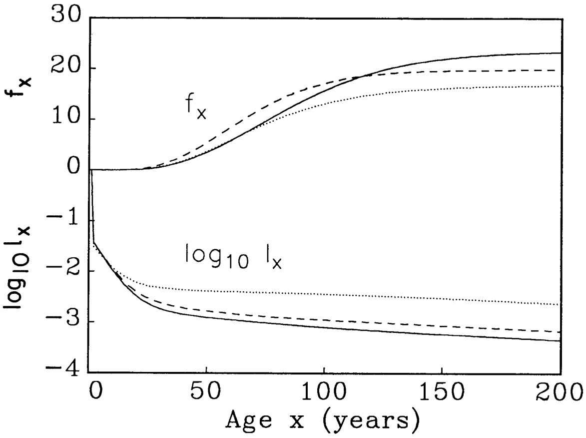

FIG. 2. Maternity function, f_x, and survivorship function, l_x, for three populations of *Astrocaryum mexicanum*. Values of $f_x/10$, $\log_{10} l_x$ for low- (solid line), medium- (dashed line), and high- (dotted line) density plots, based on data of Pinero et al. (1984). See Table 3 and Appendix 6 for details of the transition-matrix models.

How old are reproducing adults in pink lady's-slipper, Cypripedium acaule*?*

The methods in this paper were originally derived to estimate age-related traits in the pink lady's-slipper, *Cypripedium acaule,* a temperate terrestrial orchid that is long-lived and generally cannot be aged, even by destructive methods. (The complex life cycle of this species, which includes several below-ground stage classes, is described in Appendix 6.) Stage classes are summarized in Table 3. The dynamics of ≈2000 *C. acaule* ramets were followed over a 4-yr period (Cochran 1986), and the average transition, fission, and birth matrices for this population are given in Appendix 6.

Previous estimates of age in *Cypripedium acaule* have been based on limited anecdotal observations. However, estimates of individual life-spans are of interest to managers of natural areas who monitor natural populations to detect deteriorating environmental conditions or external disturbances, such as illegal harvesting (Bratton 1985). Marked reductions in longevity over predicted lifespans may indicate that intervention is necessary to preserve the population. Furthermore, models may be used to compare differences in total life-span between populations subject to different harvesting regimes to determine "acceptable" levels of external disturbance. Mean age at maturity provides a practical lower bound for the time necessary to establish (or re-establish) a population of reproductive individuals from a cohort of newborns. In species that cannot be aged or monitored from birth to maturity, our methods allow the mean age at first reproduction to be derived from stage-transition data.

Because fission occurs in the model for *C. acaule,* the conditional total life span is undefined; however, the stable age distribution, ω_t (Fig. 4a) and the stage-specific ages y_i and S_i (Table 6) provide quantitative estimates of age for this species. The sharp change in the stable age distribution (Fig. 4a) at age 4 is due to the high estimates of mortality in the seed and seedling stages, which end, on average, around age 4. The remainder of the age distribution is determined by looping between the aboveground and dormant classes. Although stages 5–8 are totally connected (i.e., $P(i, j) >$

TABLE 5. Selected life history parameters for *Dipsacus sylvestris,* based on the data of Werner and Caswell (1977) for Field A. See Table 3 and Appendix 6 for details of stage-transition matrices.*

	Newborn type 1 (dormant seeds)	Newborn type 3 (small rosettes)	Newborn type 4 (medium rosettes)	Newborn type 5 (large rosettes)
R_0	3.9605	28.951	111.89	315.15
Pr(maturity)	.011315	.082710	.31967	.90036
E(α)	3.8072	4.0053	3.3995	2.2005
SD (α)	1.1205	1.0204	.86664	.49058

* Newborn type *j* is the stage class in which individuals first appear. Pr(maturity) is a newborn's probability of surviving to enter a stage in which reproduction occurs, and α is the mean age (in years) when this occurs for individuals that survive to maturity.

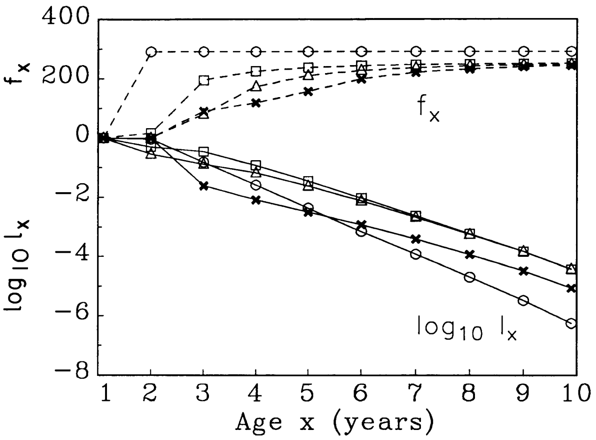

FIG. 3. Maternity function, f_x (– – –), and survivorship function, l_x (——), for four newborn types of *Dipsacus sylvestris*. Values of $f_x/100$, $\log_{10} l_x$ for type-1 (×), type-3 (△), type-4 (□) and type-5 newborns (○), based on Caswell (1989). See Table 3 and Appendix 6 for details of the transition matrix model.

0 for $i, j \in \{5, 6, 7, 8\}$), there is a marked difference between the stage-specific age distributions ($p_{i,a}$) for these classes (Fig. 4b), with a larger number of older individuals in the flowering stage classes and younger individuals in the one-leaf stage class. The differences between these distributions lead to differences in the stage-specific ages y_i and S_i (Table 6). Since $\lambda > 1$, the values of y_i are skewed towards younger ages; for instance, a flowering ramet chosen at random from the population is predicted to be 14 to 15 yr old. However, the age of residence, S_i, and its high variance, indicates that on the average a flowering ramet will reach age 39, and many will live much longer.

Using Eq. 15 the mean age at maturity for *C. acaule* is 11.1 yr. This value compares favorably with the anecdotal observation from very limited greenhouse experiments that flowering plants can be produced from seeds in 15 yr (Curtis 1943). The standard deviation of age at maturity (Eq. 16) is 8.6 yr, which implies that maturation of a cohort is highly asynchronous. Because a large part of *C. acaule*'s life cycle occurs belowground, age at maturity cannot be measured in the field, so our results provide information not otherwise available.

DISCUSSION

Stage-based demography and stage-transition models are now an established method for studying populations in which attributes other than age are the best predictor of an individual's future survival, growth and fecundity, or in which the age of individuals is difficult to determine. Their flexibility in the definition of stages, and ability to accommodate multiple modes of reproduction, has allowed stage-based studies of organisms with a wide variety of life cycles (e.g., bryozoans, corals, herbs, trees, turtles) that could not be handled as well within the standard framework of age-based demography. In addition, the stage-transition matrix model is an important approach in theoretical population biology (Geramita and Taylor 1990). However, the development of methods for analyzing the implications of a population's stage-transition matrix has been limited in comparison to available methods for life-table analysis.

Our goal in this paper has been to demonstrate that essentially *all* of the information that can be derived from a complete age-based life table can also be derived from a stage-based demographic description of a population, even for populations with multiple modes of reproduction and/or fission. This increases the information that can be extracted from a stage-based demographic study, and, as we have illustrated, it provides a common set of parameters for comparing different populations within a species or different modes of reproduction. Similarly, these methods can be applied to compare species with different life cycles (e.g.,

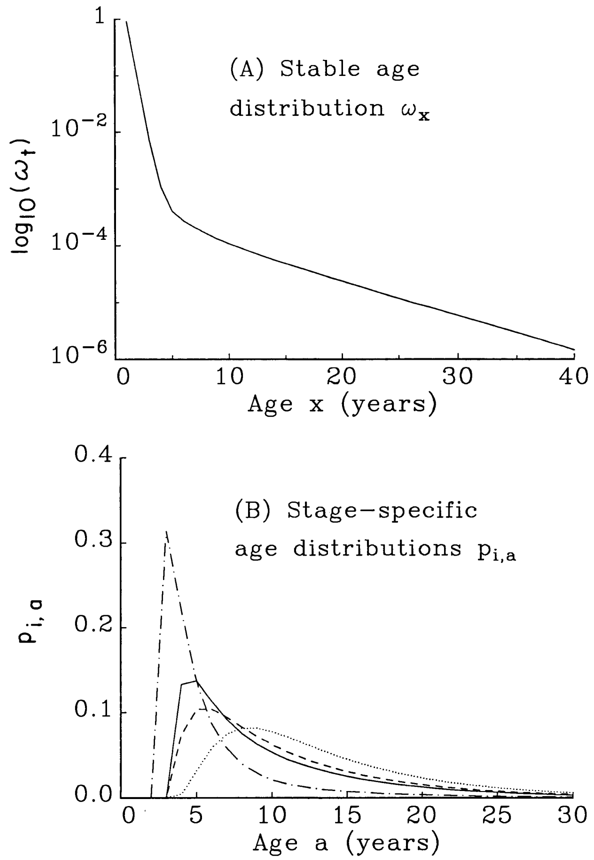

FIG. 4. Stable age distributions (ω) for *Cypripedium acaule*. (A) $\log_{10}(\omega_i)$ for ramet dynamics based on data of Cochran (1986). For details of the transition matrices, see Table 3 and Appendix 6. (B) Stage-specific stable age distributions ($p_{i,a}$) for dormant (——), one-leaf (— · —), two-leaf vegetative (– – –), and flowering (· · · · ·) ramets.

TABLE 6. Parameters of ramet population dynamics for *Cypripedium acaule,* based on the data of Cochran (1986). For details of the transition-matrix model, see Table 3 and Appendix 6.

Stage class	w_i	y_i Mean	y_i SD	S_i Mean	S_i SD
1	.93610	1.0309	(0.17839)	1.0345	(0.18887)
2	.056064	2.0309	(0.17839)	2.0345	(0.18887)
3	.0050366	3.0309	(0.17839)	3.0345	(0.18887)
4	.00047375	4.0779	(0.28472)	4.0871	(0.30178)
5	.00010755	11.091	(6.8870)	34.268	(30.885)
6	.0013973	6.8696	(4.6285)	21.721	(27.124)
7	.00053686	12.215	(7.1706)	36.044	(31.034)
8	.00028724	14.803	(7.4980)	39.302	(31.165)

Sarukhan and Gadgil 1974), to compare male vs. female life histories (e.g., Meagher 1982), or to compare geographically subdivided populations (e.g., Caswell 1989: section 4.4.4). Applying conclusions from theoretical models to actual populations is frequently difficult and should be done with caution. However, our results do provide additional means for assessing the validity of the projections generated by models derived from data.

Our results extend Caswell's (1989: section 5.6.3) derivation of R_0 and generation time measures (μ_1, $\bar{A}$, and T) from the z-transformed life-cycle graph. z-transform methods can be useful for investigating the theoretical consequences of various assumptions about life history, but their application to data may be computationally intensive (Appendix 7 and Table 7). Moreover, Caswell's (1989) assumptions limit his results to populations with a single class of newborns. This excludes plant species that reproduce both sexually and vegetatively, as well as plants reproducing by seed if there are multiple germination cohorts or if seeds germinate soon enough to generate several categories of seedlings before the next census (e.g., teasel, example 4.1 in Caswell 1989). By deriving the demographic parameters directly from the transition, birth, and fission matrices, we can make weaker assumptions and avoid the need for z-transforming and reducing the life-cycle graph.

The formulas for individual traits (such as l_x, f_x, R_0, and expected life-span) do not depend on an assumption of stable stage distribution. However, the formulas for most population attributes (e.g., the average age of individuals in a stage class) are only valid for populations that have reached stable stage distribution; consequently, they are projections of long-run behavior rather than estimates of the current situation.

The most surprising thing about our results is that they weren't discovered and exploited by population biologists years ago—the derivations are short, they use only basic matrix algebra and Markov chain theory, and very similar ideas are used in ecosystems "network analysis" (e.g., Patten 1982). The computations only require a decent set of matrix algebra routines (e.g., EISPACK, *Numerical Recipes* [Press et al. 1986], GAUSS, or MATLAB [see *Introduction* for sources]), and a modest computer (our examples all ran within minutes using GAUSS on an 8087/88 desktop or using EISPACK on a Macintosh SE). This makes it feasible to obtain numerically the sensitivity of the various parameters to changes in individual matrix entries, and to use "bootstrapping" to make rigorous statistical comparisons (e.g., between the R_0s of different populations or the f_x curves of different types of offspring). While we have not pursued it here, this approach may provide objective statistical methods for testing the adequacy of a proposed stage-transition model for a population.

In this paper we have emphasized the analysis of empirical models derived from demographic data. However, stage-transition models also have been used to address theoretical questions about the long-term dynamics of hypothetical stage-structured populations (e.g., Calvo and Horovitz 1990). Our approach may be useful for the analysis of such theoretical models, especially regarding clonal reproduction. The demographic consequences of clonal reproduction have been investigated theoretically (e.g., Caswell 1985). Our approach provides a framework for extending this theory

TABLE 7. Computational steps for reducing the z-transformed life-cycle graph.*

Species	Number of stage classes	Number of steps required	Maximum number of steps†
Caretta caretta	7	15	273
Pedicularis furbishiae	4	21	42
Dipsacus sylvestris	6	34	165
Astrocaryum mexicanum	10	38	855
Cypripedium acaule	8	52	420
Arisaema triphyllum	7	134	273

* Life cycles are from example matrices (see Appendix 6 or the following sources): *Arisaema* (Bierzychudek 1982); *Astrocaryum* (Pinero et al. 1984); *Caretta* (Crouse et al. 1987); *Cypripedium* (Cochran 1986); *Dipsacus* (Caswell 1989, Werner and Caswell 1977); *Pedicularis* (Menges 1986).

† The number of steps required to reduce the z transform of a completely connected system with the same number of stage classes (Eq. 7.1, Appendix 7).

to examine the effects of clonal growth on the evolution of life history parameters. When asexual offspring are assigned to ***F***, our methods give the life history traits of genets, making it possible to contrast the life histories and clonal growth rates of competing genets within a population, and to predict the consequences of changes in genet life history traits such as the allocation to sexual vs. asexual reproduction.

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APPENDIX 1

THE ASSUMPTIONS REQUIRED FOR CASWELL (1989).

In this appendix we clarify the assumptions required for Caswell's (1989: section 5.6.3) expressions for R_0, T, μ_1, and $\bar{A}$ in terms of the z-transformed life-cycle graph. Caswell (1989) states only one assumption: that the life-cycle graph contain no disjoint loops. Here we show, by example, that his expressions may give incorrect values unless (1) there is only one type of newborn (Caswell (1989) writes that no-disjoint-loops "corresponds" to there being only one newborn type, but our first example shows that these are not equivalent), and (2) there are no survival transitions (other than self-loops) into the newborn class. If assumption (1) fails, Caswell's expressions omit some reproductive paths that need to be included, while if (2) fails, they include paths that do not represent reproduction. However, if both (1) and (2) hold, it is apparent (by considering the *unreduced* z-transformed life-cycle graph) that the expressions Caswell (1989) derives are correct (apart from a typographical error—see below).

Consider the life-cycle graph shown in Fig. A1:a. This life cycle contains no disjoint loops (all paths must pass through stage 3), but there are two types of newborns (stages 1 and 2). Thus, the assumption that the life-cycle graph contains no disjoint loops is not equivalent to assuming that all newborns are identical. The reduced, z-transformed life-cycle graph has characteristic equation

$$1 = B_{13}P_{31}\lambda^{-2} + \frac{B_{23}P_{32}\lambda^{-2}}{1 - P_{22}\lambda^{-1}}.$$

Correcting the typographical error in Caswell's (1989) Eq. 5.50 and applying his formulas Eqs. 5.48, 5.50, and 5.51 to this system, we obtain the expressions

$$R_0\text{:}\quad B_{13}P_{31} + \frac{B_{23}P_{32}}{1 - P_{22}},$$

$$\bar{A}\text{:}\quad 2B_{13}P_{31}\lambda^{-2} + \frac{2B_{23}P_{32}\lambda^{-1}}{\lambda - P_{22}} + \frac{B_{23}P_{32}P_{22}\lambda^{-1}}{(\lambda - P_{22})^2}, \text{ and} \qquad (1.1)$$

$$\mu_1\text{:}\quad \left\{2B_{13}P_{31} + \frac{2B_{23}P_{32}}{1 - P_{22}} + \frac{B_{23}P_{32}P_{22}}{(1 - P_{22})^2}\right\} \Big/ R_0.$$

The numerical example shown in Table A1 demonstrates that the expressions for $\bar{A}$ and μ_1 are incorrect. The reason for the error can be seen by comparing the formulas with the life-cycle graph. The formulas for $\bar{A}$ and μ_1 ignore the offspring produced by the pathways 1 → 3 → 2 and 2 → 3 → 1, i.e., by pathways which are not closed loops. Thus, Caswell's methods do require assumption (1). The formula for R_0 in expression 1.1 is correct, since at stable stage distribution the number of type-i offspring produced is independent of the original type of the parent.

Next, consider the life-cycle graph with no disjoint loops and only one newborn class, shown in Fig. A1:b. The transition from stage 2 to stage 1 allows individuals to enter a newborn class through survivorship rather than reproduction. The characteristic equation for this system is $1 = P_{21}P_{12}\lambda^{-2} + P_{21}P_{32}B_{13}\lambda^{-3}$. Applying Caswell's formulas to this system results in

$$R_0\text{:}\quad P_{21}P_{12} + P_{21}P_{32}B_{13},$$

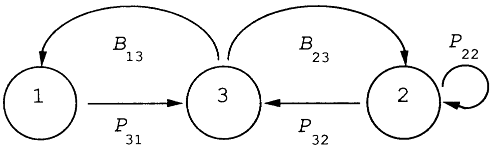
$$\bar{A}\text{:}\quad 2P_{21}P_{12}\lambda^{-2} + 3P_{21}P_{32}B_{13}\lambda^{-3}, \text{ and} \qquad (1.2)$$

$$\mu_1\text{:}\quad (2P_{21}P_{12} + 3P_{21}P_{32}B_{13})/R_0.$$

Each expression contains a term $P_{21}P_{12}$, which does not represent a reproductive pathway. In addition, the pathway 1 → 2 → 3 → 1 has not been scaled to include the time lag contributed by looping between class 1 and 2. A numerical example (Table A1) confirms that this can lead to incorrect values. Thus, Caswell's formulas also require assumption (2). Assumptions (1) and (2) are satisfied in all examples given in Caswell (1989: section 5.6.3). However, the numerical values given there for $\bar{A}$ should be multiplied by λ^2 to correct for the typographical error in his Eq. 5.50 which should read

$$\bar{A} = -\lambda \sum_i \left.\frac{\partial L^{(i)}}{\partial \lambda}\right|_{\lambda=\lambda_1}. \qquad (1.3)$$

(A) Two newborn classes



(B) Survival into newborn class

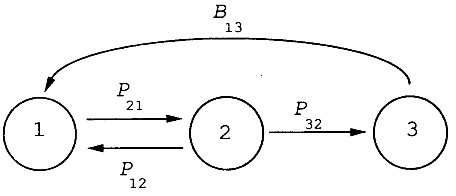


FIG. A1. (A) Life-cycle graph with no disjoint loops, but 2 newborn classes (stage 1 and stage 2). (B) Life-cycle graph with no disjoint loops, 1 newborn class (stage 1), but survival into the newborn stage.

TABLE A1. Net reproductive rate and generation times. Example 1: $P_{31} = 0.4$, $P_{22} = 0.3$, $P_{32} = 0.5$, $B_{13} = 0.9$, and $B_{23} = 0.6$; all other entries are 0. Example 2: $P_{21} = 0.72$, $P_{12} = 0.1667$, $P_{32} = 0.8$, and $B_{13} = 2.75$; all other entries are 0. Caswell (1989) refers to the formulas for net reproductive rate and generation time presented in Caswell (1989: section 5.6.3). For further details, see Appendix 1.

		R_0	T	$\bar{A}$	μ_1
Example 1:	Actual values	0.7886	2.254	2.280	2.233
	Caswell (1989)	0.7886	2.254	4.675	2.776
Example 2:	Actual values	1.800	3.224	3.182	3.273
	Caswell (1989)	1.704	2.923	2.917	2.930

APPENDIX 2

SOME IDENTITIES FOR CONVERGENT MATRICES

Let $\boldsymbol{M}$ be a square, convergent matrix. It is a standard result of linear algebra (e.g., Isaacson and Keller 1966) that $(\boldsymbol{I} - \boldsymbol{M})$ is invertible and

$$\sum_{t=0}^{\infty} \boldsymbol{M}^t = (\boldsymbol{I} - \boldsymbol{M})^{-1}. \tag{2.1}$$

This is the matrix analog to the geometric series $1 + r + r^2 + \ldots = (1 - r)^{-1}$ for $|r| < 1$. We also use the identities

$$\sum_{t=0}^{\infty} (t + 1)\boldsymbol{M}^t = (\boldsymbol{I} - \boldsymbol{M})^{-2}, \quad \text{and} \tag{2.2}$$

$$\sum_{t=0}^{\infty} (t + 1)^2\boldsymbol{M}^t = (\boldsymbol{I} + \boldsymbol{M})(\boldsymbol{I} - \boldsymbol{M})^{-3}. \tag{2.3}$$

Eq. 2.2 is the matrix analog of the identity

$$1 + 2r + 3r^2 + \ldots + (n + 1)r^n + \ldots = (1 - r)^{-2}$$

for $|r| < 1$. To prove Eq. 2.2, note that

$$\left[\sum_{t=0}^{\infty} (t + 1)\boldsymbol{M}^t\right](\boldsymbol{I} - \boldsymbol{M})$$

$$= \sum_{t=0}^{\infty} (t + 1)\boldsymbol{M}^t - \sum_{t=0}^{\infty} (t + 1)\boldsymbol{M}^{t+1}$$

$$= \boldsymbol{I} + \sum_{t=1}^{\infty} (t + 1)\boldsymbol{M}^t - \sum_{t=1}^{\infty} t\boldsymbol{M}^t$$

$$= \boldsymbol{I} + \sum_{t=1}^{\infty} \boldsymbol{M}^t = (\boldsymbol{I} - \boldsymbol{M})^{-1}.$$

Multiplying through on the right by $(\boldsymbol{I} - \boldsymbol{M})^{-1}$ gives Eq. 2.2. The formal manipulations above can be made completely rigorous by considering partial sums. Using Eq. 2.2, essentially the same argument can be used to show that

$$\left[\sum_{t=0}^{\infty} (t + 1)^2\boldsymbol{M}^t\right](\boldsymbol{I} - \boldsymbol{M}) = (\boldsymbol{I} + \boldsymbol{M})(\boldsymbol{I} - \boldsymbol{M})^{-2},$$

and then multiplying through on the right by $(\boldsymbol{I} - \boldsymbol{M})^{-1}$ gives Eq. 2.3.

APPENDIX 3

POPULATION MEASURES OF CONDITIONAL TOTAL LIFE-SPAN AND AGE AT MATURITY

In this appendix we derive the mean and variance of the total life-span conditional on passing through stage i, and the age at maturity, for populations with multiple types of newborns at stable stage distribution.

For an individual chosen at random from the current cohort of newborns, let τ_i be the (random) age at which that individual first enters stage i, or else $\tau_i = +\infty$ if stage i is not reached before death, and let N be the stage from which the individual was drawn. Then,

$$\begin{aligned} &\mathrm{E}(\tau_i \mid \tau_i < \infty) \\ &= \sum_{j=1}^{n} \mathrm{E}(\tau_i \mid \tau_i < \infty, N = j)\Pr(N = j \mid \tau_i < \infty) \\ &= \sum_{j=1}^{n} \mathrm{E}(\tau_{ij} \mid \tau_{ij} < \infty)\Pr(N = j \mid \tau_i < \infty). \end{aligned}$$

Applying Bayes' theorem,

$$\begin{aligned} \Pr(N = j \mid \tau_i < \infty) &= \frac{\Pr(\tau_i < \infty \mid N = j)\Pr(N = j)}{\sum_{k=1}^{n} \Pr(\tau_i < \infty \mid N = k)\Pr(N = k)} \\ &= \frac{\Pr(\tau_i < \infty \mid N = j)b_j}{\sum_{k=1}^{n} \Pr(\tau_i < \infty \mid N = k)b_k} \\ &= \frac{\Pr(\tau_{ij} < \infty)b_j}{\sum_{k=1}^{n} \Pr(\tau_{ik} < \infty)b_k}. \end{aligned}$$

Therefore, the expected time to first reach stage class i is

$$\mathrm{E}(\tau_i \mid \tau_i < \infty) = \frac{\sum_{j=1}^{n} \mathrm{E}(\tau_{ij} \mid \tau_{ij} < \infty)\Pr(\tau_{ij} < \infty)b_j}{\sum_{k=1}^{n} \Pr(\tau_{ik} < \infty)b_k}. \tag{3.1}$$

Substituting into Eq. 3.1 the expressions obtained for $\mathrm{P}(\tau_{ij} < \infty)$ and $\mathrm{E}(\tau_{ij} \mid \tau_{ij} < \infty)$ in the section on conditional total life-span, gives

$$\mathrm{E}(\tau_i \mid \tau_i < \infty) = \frac{\sum_{j=1}^{n} (I - D_i)^{-2}(i, j)b_j}{\sum_{k=1}^{n} (I - D_i)^{-1}(i, k)b_k}. \tag{3.2}$$

Since $\Lambda_i = \mathrm{E}(\tau_i + \Omega_i \mid \tau_i < \infty) = \mathrm{E}(\tau_i \mid \tau_i < \infty) + L(i)$, Eq. 25 follows. Applying the arguments above to τ_i^2 in place of τ_i, gives

$$\mathrm{Var}(\tau_i \mid \tau_i < \infty) = \frac{\sum_{j=1}^{n} (I + D_i)(I - D_i)^{-3}(i, j)b_j}{\sum_{j=1}^{n} (I - D_i)^{-1}(i, j)b_j} - [\mathrm{E}(\tau_i)]^2. \tag{3.3}$$

The future of an individual in stage i is independent of its past (by assumption), hence

$$\mathrm{Var}(\tau_i + \Omega_i \mid \tau_i < \infty) = \mathrm{Var}(\tau_i \mid \tau_i < \infty) + \mathrm{Var}(\Omega_i). \tag{3.4}$$

The age at maturity, α, is the age at which a randomly chosen newborn first enters the set K of stages with positive fecundity. Consequently, the mean and variance for α may be obtained simply by substituting $\boldsymbol{Q}$ for $\boldsymbol{D}_i$ and α_j for τ_{ij} in the derivations above. This gives Eq. 26 in the text, and

$$\mathrm{Var}(\alpha \mid \alpha < \infty) = \frac{\sum_{i\in K} \sum_{j=1}^{n} [(I + Q)(I - Q)^{-3}](i, j)b_j}{\sum_{i\in K} \sum_{j=1}^{n} (I - Q)^{-1}(i, j)b_j} - [\mathrm{E}(\alpha)]^2. \tag{3.5}$$

APPENDIX 4

PROOF THAT $\lambda^{-1}\boldsymbol{C}$ IS CONVERGENT

Recall that a matrix is convergent if and only if its eigenvalues are all <1 in magnitude. To show that $\lambda^{-1}\boldsymbol{C}$ is convergent, recall that

$$\frac{\partial\lambda}{\partial A(i,j)} = \frac{v_i w_j}{\langle \boldsymbol{v}, \boldsymbol{w}\rangle} \geq 0$$

(Caswell 1989); hence Eq. 1 can be re-expressed as

$$\langle \boldsymbol{v}, \boldsymbol{w}\rangle \sum_{i=1}^{n} \sum_{j=1}^{n} B(i,j) \frac{\partial\lambda}{\partial A(i,j)} > 0.$$

This implies that for some (i, j), both $B(i, j)$ and $\partial\lambda/\partial A(i, j)$ are positive. Since $\boldsymbol{C} = \boldsymbol{A} - \boldsymbol{B}$, it follows that the dominant eigenvalue of $\boldsymbol{C}$ is $<\lambda$. The eigenvalues of $\lambda^{-1}\boldsymbol{C}$ are those of $\boldsymbol{C}$ divided by λ; hence the dominant eigenvalue of $\lambda^{-1}\boldsymbol{C}$ is <1 as required.

APPENDIX 5

AGE COMPOSITION OF STAGES WITH $w_i = 0$

We show here how the asymptotic age composition of all stages can be obtained, in cases where not all stages are represented in the stable stage distribution, $\boldsymbol{w}$. By renumbering stages (if necessary), we can assume that $w_i = 0$ for $i = 1, 2, \ldots, m$, while $w_i > 0$ for $i = m + 1, \ldots, n$. Call these "absent" and "present" stages, respectively. At stable stage distribution, there is no flow of individuals from absent to present stages. Absent stages can therefore be deleted from the model without affecting the present stages, and the age distributions of the present stages can be found by applying our results to the reduced model in which all stages are present. The absent stages cannot be receiving any direct or indirect input from any present stages, or else they would be present (formally, since $\lambda^t w_i = \Sigma_j A^t(i, j)w_j$ for any $t \geq 1$, $A^t(i, j)$ must be zero whenever $w_i = 0$ and $w_j > 0$). Consequently, the absent stages are unaffected by deletion of the present stages. The reduced submodel consisting of only absent stages can then be used to compute the age distribution of those stages, repeating the reduction to submodels if necessary.

APPENDIX 6

THE DERIVATION OF TRANSITION MATRICES FOR THE EXAMPLES

Astrocaryum mexicanum

(all data are from Pinero et al.[1984])

A. mexicanum grows continuously throughout the year, producing new leaves and thus extending the length of its trunk. Individuals pass directionally through a series of size classes (Table 2), beginning as seedlings, then nonreproductive juveniles, and, finally, adults capable of reproduction.

Stage classes M6, M7, M8, M9, and M10 were pooled to improve sample size and eliminate missing data for some of the larger stages. Mortality is low for large adults. Although mortality appears to increase at higher densities, large-adult mortality did not differ significantly between the high (3 out of 324 deaths·individual^{-1}·yr^{-1}), medium (1/204 deaths·individual^{-1}·yr^{-1}), and low-density plots (0/108 deaths·individual^{-1}·yr^{-1}). Hence, the data were pooled over all densities to give an estimate of $P_{10} = 0.995$, which was used in all three matrices. Note that the use of this estimate is conservative, in that it does not contribute to the observed differences between densities. Fission does not occur. Stage classes were chosen so that growth from stage class i into stage classes $i + 2$ up to 10 cannot occur in one time step. In addition, since the *A. mexicanum* stage classes are based on trunk length, survival transitions from stage class i into stage classes 1 up to $i - 1$ were also impossible. Thus, many entries in the survival matrix $\boldsymbol{P}$ are structurally zero. At all densities, the survival matrix $\boldsymbol{P}$ has non-zero entries only on the diagonal ($P(i, i)$, representing survival without growth into a larger stage-class) and on the subdiagonal ($P(i + 1, i)$, representing growth into a larger stage-class). All non-zero entries of the birth matrices are in the first row ($B(1, i)$, representing seed production). The entries in the survival and birth matrices that are not structurally zero are shown in Table A2.

TABLE A2. Structurally nonzero entries in the survival matrix $\boldsymbol{P}$ and the birth matrix $\boldsymbol{B}$ for populations of *Astrocaryum mexicanum* at 3 densities. $P(i,i)$, represents survival without growth into a larger stage class and $P(i+1,i)$ represents growth into a larger stage class. Entries in the first row of the birth matrix, $B(1,i)$, represent seed production. All values are based on data of Pinero et al. (1984). See Table 3 for stage classes and Appendix 6 for details of the calculation of these values.

	High density			Medium density			Low density		
Stage i	$P(i,i)$	$P(i+1,i)$	$B(1,i)$	$P(i,i)$	$P(i+1,i)$	$B(1,i)$	$P(i,i)$	$P(i+1,i)$	$B(1,i)$
1	0	.037349	0	0	.03629	0	0	.030332	0
2	.83093	.015881	0	.84127	.014582	0	.85001	.026738	0
3	.89666	.048969	0	.91636	.058131	0	.93928	.049660	0
4	.95944	.029778	0	.93735	.051565	0	.94548	.048040	0
5	.90496	.082074	0	.91462	.065923	0.18385	.91850	.081500	0.33
6	.91348	.086520	1.4792	.84680	.14240	4.222	.93130	.068700	0.918
7	.90553	.094467	8.1560	.87250	.12000	8.41	.86362	.13637	8.0875
8	.87733	.088200	9.9513	.84332	.14800	8.8405	.91225	.87750	16.606
9	.88642	.11358	14.259	.91303	.086966	16.676	.87867	.12133	13.068
10	.995	0	23.594	.995	0	19.904	.995	0	16.875

TABLE A3. Survival matrix ***P*** for *Dipsacus sylvestris. P(i,j)*, represents the probability that an individual is in stage class *i* at time *t* given that the individual is in stage class *j* at time $t - 1$. All values are based on data of Werner and Caswell (1977). See Table 3 for stage classes and Appendix 6 for details of the calculation of these values.

	From class *j*					
To class *i*	1	2	3	4	5	6
1	0	0	0	0	0	0
2	0.966	0	0	0	0	0
3	0.013	0.010	0.125	0	0	0
4	0.007	0	0.125	0.238	0	0
5	0.008	0	0.038	0.245	0.167	0
6	0	0	0	0.023	0.750	0

Dipsacus sylvestris
(all data are from Werner and Caswell [1977], field A)

D. sylvestris is a semelparous herbaceous perennial that reproduces totally by seeds. Seeds produced in the spring either remain dormant or else germinate and grow into rosettes of varying sizes by the next spring. Thus, newly produced seeds do not appear as a stage class in the stage-transition model of the population. Instead, the dormant seeds and the various sizes of first-year rosettes appear as several classes of newborns in the model (Werner and Caswell 1977, Caswell 1989); the stage classes are described in Table 2. Rosettes increase in size for an indeterminate number of years until the individual flowers and dies (Werner 1975).

Teasel was sown in eight fields representing several habitats, and the resulting populations were followed for 5 yr (Werner and Caswell 1977). The stage class for seeds from Werner and Caswell (1977) were absorbed as suggested in Caswell (1989) to correct for germination and establishment times of <1 yr. Fission does not occur. The survival matrix is shown in Table A3. There are four nonzero entries in the birth matrix: $B(1, 6) = 322$; $B(3, 6) = 3.45$; $B(4, 6) = 23.9$; and $B(5, 6) = 0.682$.

Cypripedium acaule
stage classes are given in Table 2

Fruits of *C. acaule* ripen in the late autumn and disperse seeds over the next one to two years. The long-term viability of the seed bank is unknown, but seeds 2 yr old have been successfully germinated on artificial culture media (Curtis 1943). In nature, *C. acaule* requires a mycorrhizal associate for seed germination and seedling establishment; it is difficult to grow from seed under field conditions. Once the seeds germinate, they form a protocorm. Individuals remain in the corm stage for an indeterminant period of time (at least 2 yr) before forming their first aboveground leaf (Curtis 1943). Individuals eventually produce two leaves and may then flower. Rhizomes may produce additional one-leafed, two-leafed or flowering modules (or ramets), which remain attached to the parent and do not function independently; occasionally, vigorous individuals may produce as many as 25 ramets from a single crown. We consider the production of additional ramets from a mature crown to be fission. Individuals may also be dormant for ≥1 yr, producing no above ground parts (Cochran 1986).

Values for the transitions P_{21}, P_{32}, P_{43}, P_{53}, P_{44}, and P_{54} were estimated from data in Curtis (1943). The remaining entries in ***P*** and the entries in ***F*** are averages of the ramet dynamics for 1982–1983, 1983–1984 and 1984–1985 (Cochran 1986); "death" of a ramet occurred in year *t* when all ramets in a genet failed to appear for three consecutive years (i.e., in year t, $t + 1$, and $t + 2$). The survival matrix is shown in Table A4. There are 10 non-zero entries in the fission matrix: $F(6, 5) = 0.080484$; $F(6, 6) = 0.00043178$; $F(6, 7) = 0.0031434$; $F(6, 8) = 0.013304$; $F(7, 5) = 0.046652$; $F(7, 6) = 0.00043687$; $F(7, 7) = 0.0033932$; $F(7, 8) = 0.0556$; $F(8, 7) = 0.0010412$; $F(8, 8) = 0.030455$. There is one non-zero entry in the birth matrix: $B(1, 8) = 3519.057$ is the average probability of fruit set for 1982, 1983, and 1984 (Cochran 1986) times an estimate of seeds per fruit (Ricker in Withner 1959).

TABLE A4. Survival matrix ***P*** for *Cypripedium acaule. P(i,j)*, represents the probability that an individual is in stage class *i* at time *t* given that the individual is in stage class *j* at time $t - 1$. All values are based on data of Cochran (1986) and Curtis (1943). See Table 3 for stage classes and Appendix 6 for details of the calculation of these values.

	From class *j*							
To class *i*	1	2	3	4	5	6	7	8
1	.033333	0	0	0	0	0	0	0
2	.066667	0	0	0	0	0	0	0
3	0	.1	0	0	0	0	0	0
4	0	0	.1	.05	0	0	0	0
5	0	0	0	0	.22426	.036471	.0506	.060837
6	0	0	.1	.1	.3617	.6452	.086007	.010269
7	0	0	0	0	.38592	.10042	.61083	.22430
8	0	0	0	0	.018756	.002606	.20295	.68171

APPENDIX 7

STEPS REQUIRED FOR REDUCING THE *z*-TRANSFORM

Computing the reduced *z*-transform of a completely connected *n*-stage life-cycle graph (i.e., all transitions are nonzero) by the procedures in Caswell (1989: section 5.2), requires

$$\sum_{i=1}^{n-1} 3i^2 = \frac{n(n-1)(2n-1)}{2} \qquad (7.1)$$

steps; with *j* stages present, absorbing self-loops requires $j(j - 1)$ computations, then removing a single stage involves $(j - 1)^2$ computations, and consolidating the resulting duplicate pathways takes $(j - 1)(j - 2)$ computations (leaving a completely connected $j - 1$ stage life-cycle graph) for a total of $(j + j - 1 + j - 2)(j - 1) = 3(j - 1)^2$ computations. Thus, iterating until the graph is reduced to a single stage with a single loop is an order-n^3 process for a population with *n* stage-classes.