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In the following article, Professor Carmine Lanciani discusses some options for using life tables in general biology or ecology courses and calculating or estimating reproductive values. I think you will find Professor Lanciani's adjustments to the formulae can allow students more time to think about the ecological concepts underlying reproductive values and spend less time doing the mathematical manipulations (no offense to the mathematicians among us).—Ed.

A SIMPLE EQUATION FOR PRESENTING REPRODUCTIVE VALUE TO INTRODUCTORY BIOLOGY AND ECOLOGY CLASSES

Reproductive value, a measure of the relative reproductive potential of an individual at any age, is a useful ecological concept that can be applied to diverse subjects, such as optimization of life histories, colonization of islands, and management of exploited populations. However, complexity of the reproductive value equation often causes instructors to ignore or poorly handle the concept in introductory biology and ecology classes. The original equation for reproductive value (Fisher 1930) applies to continuous breeders, and most attempts to convert Fisher's formula to a discrete form suitable for seasonal breeders have led to this

commonly cited equation (e.g., MacArthur and Wilson 1967, Mertz 1970, Wilson and Bossert 1971, Pianka 1994, Gotelli 1995, Smith 1996):

$$v_x = \frac{\sum_{y=x}^{\infty} e^{-ry} l_y m_y}{e^{-rx} l_x} \quad (1)$$

In this equation, which uses data from an age-specific or cohort life table such as Table 1, v_x is reproductive value of a female at age x , l_x is the proportion of newborn females that survive to age x , m_x is the average number of daughters born to a female at age x , and r (often symbolized r_m) is a per capita rate of increase called the intrinsic rate of natural increase. The parameter l_x is found by dividing the number of females that survive to age x , S_x , by the number alive at age 0, S_0 . The parameter m_x is found by dividing the total number of daughters born to all females at age x , symbolized B_x here, by S_x . The intrinsic rate of natural increase can be calculated from life table data using standard methods (Ricklefs 1990) or from the natural log of the finite rate of increase. The finite rate of increase, λ , is the dominant eigenvalue of the projection matrix and also is equal to N_{t+1}/N_t , as shown in the exponential growth equation in which N_t is population size (of females) at time t .

Most students in introductory biology and ecology classes struggle with Eq. 1. Even seasoned ecologists may have trouble translating this equation or its continuous-form predecessor into words (Caswell 1989). But Eq. 1 can be made more student-friendly by changing the derived functions l and m_x to their basic life table equivalents S_x/S_0 and B_x/S_x , replacing e^r with λ , combining similar terms, and changing summation-sign subscripting from $y = x$ to $i = 0$:

$$v_x = \frac{\sum_{i=0}^{\infty} \lambda^{-i} B_{x+i}}{S_x} \quad (2)$$

An advantage of Eq. 2 is its relative transparency. It shows, more clearly than does Eq. 1, that reproductive value is defined as a weighted average of present ($i = 0$) and future ($i > 0$) reproduction by a female at age x . The weighting factor, λ^{-i} , weights reproduction according to its timing and can be viewed as the relative "value" of a daughter born i time units in the future when population size will be N_{t+i} . More specifically, the weighting factor is equivalent to a future daughter's proportional representation ($1/N_{t+i}$), relative to a present daughter's proportional representation ($1/N_t$). Thus, each of the B_{x+i} daughters is weighted by $(1/N_{t+i})/(1/N_t)$, which equals N_t/N_{t+i} or λ^{-i} . Consequently, future reproduction, i.e., reproduction at time $t + i$, is weighted less than present reproduction, i.e., reproduction at time t , when the population is growing ($N_t < N_{t+i}$), but is weighted more when the population is declining ($N_t > N_{t+i}$).

The definition of reproductive value discussed above differs from that of another common approach to reproductive value, one based on matrix algebra. This approach has been elucidated by Caswell (1989) and others who have equated reproductive value to the left eigenvector of the projection matrix. The difference between these two views of reproductive value can be seen in Table 1, which shows that v_x values from Eqs. 1 and 2 are higher than those from the matrix approach by an amount equal to m_x . Thus, while Eqs. 1 and 2 factor in reproduction from age x to the end of life, the matrix approach does so only from age $x + 1$ to the end of life. To build a simple equation compat-

Table 1. Hypothetical life table of a seasonal breeder from which reproductive value, v_x , is calculated using Eqs. 1, 2, and 3, and the matrix approach. Life table symbols are x , age units; S_x , number of females that survive to age x ; B_x , total number of daughters born to all females at age x ; l_x , proportion of newborn females that survive to age x ; and m_x , average number of daughters born to a female at age x . The intrinsic rate of natural increase, r , is 0.37 and the finite rate of increase, λ , is 1.45 in this example.

x	S_x	B_x	l_x	m_x	Reproductive value from		
					Eqs. 1, 2	Eq. 3	Matrix approach
0	100	0	1.0	0	1.00	1.00	1.00
1	60	0	0.6	0	2.41	2.41	2.41
2	50	150	0.5	3	4.20	1.20	1.20
3	40	80	0.4	2	2.17	0.17	0.17
4	10	10	0.1	1	1.00	0.00	0.00
5	0						

ible with this alternative view of reproductive value, one need change only the indexing in Eq. 2 from $i = 0$ to $i = 1$:

$$v_x = \frac{\sum_{i=1}^{\infty} \lambda^{-i} B_{x+i}}{S_x} \quad (3)$$

The matrix approach and Eq. 3 then both define reproductive value as a weighted average of future reproduction by a female at age x , and they give equivalent values of v_x (Table 1).

The simplicity of Eqs. 2 and 3 may help introductory biology and ecology teachers present reproductive value to their students. Of these two equations, Eq. 3 may be preferable because it more closely matches Fisher's (1930) concept of reproductive value of individuals as "the present value of their future offspring."

Finally, other useful parameters, such as net reproductive rate R_0 and cohort generation time T_c , can be similarly cast in terms of S_x and B_x rather than l_x and m_x (Lanciani 1987). Although abandoning the familiar l_x and m_x is unconventional and may seem ill advised to some, the advantages of using S_x and B_x may outweigh any disadvantages in the undergraduate classroom because the resulting equations rely upon the most basic of life table data; they involve fewer symbols and exponents than do alternative equations, leading to easier calculation; and they can be easily interpreted and related to parameter definitions.

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