"Biennials": A Reply to Kelly

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"BIENNIALS": A REPLY TO KELLY

Though "biennials," or more correctly semelparous perennials, are rare in the plant kingdom as a whole (Hart 1977), they are particularly abundant in certain families and in those temperate habitats where gaps occur intermittently. I have suggested that these two features of the semelparous perennial life history might be understood by using a slight modification of Charnov and Schaffer's (1973) equations for the relative rates of increase for annuals and biennials and by considering the allometry of seed yield in semelparous perennials (Silvertown 1983). Kelly (1985) challenged these conclusions on two counts.

Kelly's more fundamental objection is that it is inappropriate to use the annual rate of increase λ as a measure of the fitness of different life histories because "one does not tend to find continually increasing populations in the field. Most real populations almost certainly spend as much time in decline as they do in expansion." (Kelly 1985, p. 476.) This is a misinterpretation of the meaning of λ, which although generally referred to as the rate of increase, can of course assume values less than 1 and hence measure changes in declining populations also. Indeed, van der Meijden and van der Waals-Kooi (1979) used λ correctly to describe the dynamics of declining populations of *Senecio jacobaea*.

The second, more interesting objection Kelly raised concerns whether the life span of a plant (living n years) should enter into the calculation of its fitness if the opportunities for establishment are determined by the frequency with which gaps (establishment sites) appear. The equations given by Silvertown (1983) for the rates of increase of an annual and a biennial were, respectively,

$$\lambda_a = (C_1 S_a)^{1/x}, \quad (1)$$

$$\lambda_b = (C_1 C_2 S_b)^{1/(x+1)}, \quad (2)$$

where C_1 and C_2 are the survivorship of plants through year 1 and year 2, S_a and S_b are the number of seeds produced by an annual and by a biennial, and x is the mean time interval between gaps. Kelly claimed that the exponent $1/(x + 1)$ in equation (2) is incorrect because it allows for the fact that biennials take a year longer to produce a seed crop than an annual, which he regarded as irrelevant when $x \neq 1$. Essentially, he argued that when $x \geq 2$, the seeds of a biennial (produced in its second year) are ready and waiting for the next gap, and hence no opportunities for establishment will be missed by such plants taking two years to reproduce instead of one. He concluded from this that biennials are at no disadvantage in environments where establishment is confined to periodic gaps in the vegetation. Kelly stated, however, that "when x is small (e.g., 2) and the variance is large, there may be a significant proportion of years when gaps are created in

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two consecutive years'' (p. 476), and he acknowledged that this is a disadvantage to the biennial because its seeds are not available to colonize such a gap. Nevertheless, Kelly did not calculate the size of this fitness disadvantage because ''the mathematics describing such a model are complex, because they must take account of the proportion of gaps which the biennial misses'' (p. 476). The mathematics may be simplified to yield an approximate solution, which shows Kelly's conclusion (and a similar point made in Reinartz 1984) to be incorrect.

First, we reduce the model to its simplest and most general form. If, following Kelly, we set $C_1S_a = C_1C_2S_b = I$, then equations (1) and (2) become

$$\lambda_a = I^{1/x}, \tag{3}$$

$$\lambda_b = I^{1/(x+1)}, \tag{4}$$

or, for the general case of a plant living n years,

$$\lambda_n = I^{1/[x+(n-1)]}. \tag{5}$$

Kelly was correct that this equation is inaccurate because it does not allow for the occasions when n coincides exactly with x. To remedy this, the denominator in the exponent of equation (5) should be kx, where k is the integer number of gap cycles such that $kx \geq n \geq (k - 1)x$. In biological terms, $1/kx$ is the frequency with which a semelparous perennial living n years is able to find a gap in which to germinate, allowing for any difference between n and x. The corrected equation is

$$\lambda_n = I^{1/kx}, \tag{6}$$

where x is a mean with a binomial variance. Gaps occur with a mean interval x and hence will occur in any particular year with a probability $1/x$. The probability of there being no gap in a particular year is $1 - 1/x$, and hence the probability q of there being no gap in n years (except the ''natal'' gap in the first year) is $q = (1 - 1/x)^{n-1}$. The probability p that one or more gaps (in addition to the natal gap) occurs in n years is $1 - q$, or $p = 1 - (1 - 1/x)^{n-1}$. Gaps are most often missed when x is small or n large. Most demographic studies of biennials show that n is usually greater than 2 (Silvertown 1984; Kelly 1985), but as yet we have no information on typical gap frequencies in ''biennial'' habitats.

We now need an expression for the contribution made to λ_n on those p occasions when gaps are missed. Ideally, to take full account of the variance of x, this expression should include the higher-order terms of the binomial expansion of $(1/x + 1 - 1/x)^n$. As Kelly said, this would lead to a rather involved solution to a basically simple question; rather, consider the situation in which a gap occurs at an interval a year earlier than the mean gap interval x. A plant is, by definition, able to exploit a gap occurring kx years after its germination. It will miss an opportunity in year $kx - 1$ by one year and will have to wait another period of x years for the next gap, making a wait of $kx - 1 + x$ years in all and producing a contribution to the yearly rate of increase,

$$p(I)^{1/(kx-1+x)}. \tag{7}$$

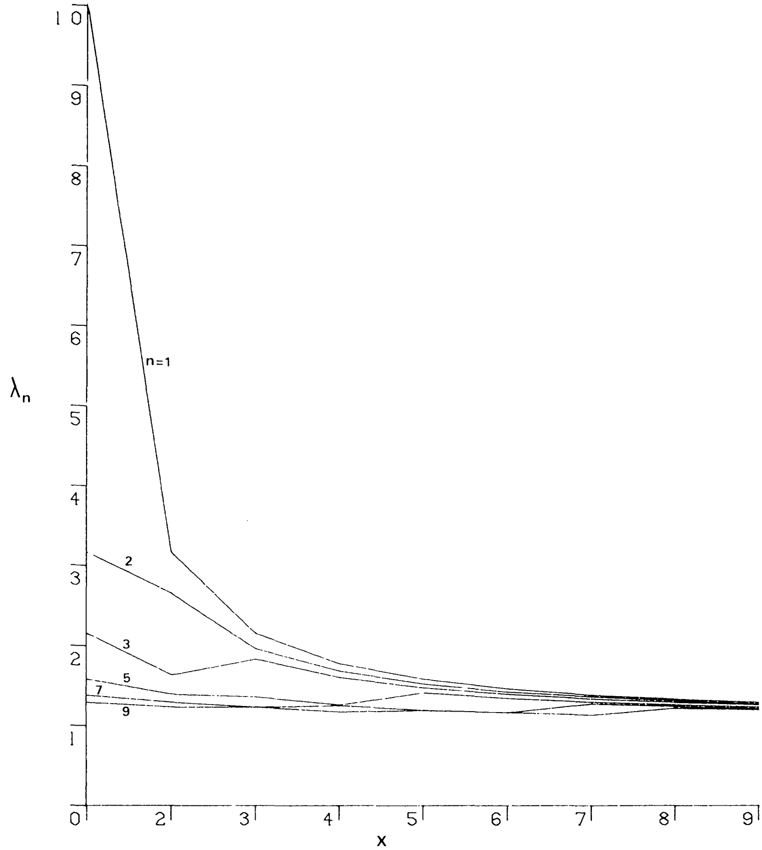

FIG. 1.—The influence of gap frequency x on the annual rate of population increase λ_n for semelparous plants living 1, 2, 3, 5, 7, and 9 yr as calculated from equation (8) (I = 10).

Remembering that $p = 1 - q$, we now obtain an expression for the rate of increase of a semelparous perennial that allows for the distribution of gap frequency around a mean value x. This is the sum of equation (6), weighted by the probability (q) that gaps will not be missed, and of expression (7):

$$\lambda_n = q(I)^{1/kx} + p(I)^{1/(kx-1+x)}. \tag{8}$$

Ignoring the higher terms of the binomial distribution of x in equation (8) does not alter the case for true biennials ($n = 2$), but for other semelparous perennials ($n > 2$), it biases the result in favor of Kelly's point. The behavior of equation (8) is shown in figure 1. It shows that the rate of increase (and hence the fitness) of semelparous perennials ($n > 1$) is significantly lower than that of annuals ($n = 1$) in habitats where establishment can only occur in gaps. The original conclusions of Silvertown (1983) stand, most especially when the common situation of $n \geq 3$ is true.

It should also be noted that, for all values of n, the highest values of λ_n are attained when the habitat is permanently open ($x = 1$). If the variance of x were of little importance, then there would be no difference in λ_2 for a true biennial whether $x = 1$ or $x = 2$. In fact (with $I = 10$), the values are $\lambda_2 = 3.162$ and $\lambda_2 = 2.658$, respectively, a 16% difference caused by plants missing gaps as a result of the variance of x.

Plant life histories are the product of natural selection, environmental contingencies (such as the frequency of gaps), and morphological constraints, all of which entered into the original argument I constructed. Our understanding will always be shallow unless we can explain the "sometimes" with which we so often have to qualify our observations in ecology. Even in the tiny question of "biennial" life history, I would be the last to claim that current models match up to the sophistication of the problem, but one thing seems certain: gap frequency sometimes does matter.

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