A General Model of Comparative Fecundity for Semelparous and Iteroparous Life Histories

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The American Naturalist, Vol. 118, No. 1 (Jul., 1981), 27-36.

A GENERAL MODEL OF COMPARATIVE FECUNDITY FOR SEMELPAROUS AND ITEROPAROUS LIFE HISTORIES

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The number of reproductive episodes before death is a key life-history character. Biologists have long considered the distinction between life histories with a single reproductive episode (semelparity) and those with multiple episodes (iteroparity) particularly important (see Stearns 1976). Both life histories are widespread in the plant and animal kingdoms. The evolution of these two life histories has been the subject of several theoretical models. Cole (1954) and Charnov and Schaffer (1973) have explored demographic explanations. After a critical review of these models, I will present a general model of comparative fecundity for semelparous and iteroparous life histories.

PREVIOUS MODELS

As used in these earlier models, the term *annual* refers to semelparous life histories with a generation time of one year, and *perennial* refers to life histories in which reproduction occurs yearly after a 1-yr development time.

Cole (1954, p. 118) stated that "for an annual species, the absolute gain in intrinsic population growth that can be achieved by changing to the perennial habit would be exactly equivalent to adding one more individual to the average litter size" (eq. [1]).

$$B_A = B_P + 1, \tag{1}$$

where B_A = fecundity of the annual, and B_P = yearly fecundity of the perennial.

Charnov and Schaffer (1973) analyzed this situation with a model which allowed for differential juvenile and adult survivorships and produced equation (2).

$$B_A = B_P + \frac{P}{C}, \tag{2}$$

where P = adult survivorship, and C = juvenile survivorship. They therefore suggested that "Cole's result be modified to read as follows: 'For an annual species, the absolute gain in intrinsic growth rate that can be achieved by changing to the perennial habit would be exactly equivalent to adding P/C individuals to the average litter size' " (p. 792). Cole's result is the special case where adult and

juvenile survivorships are assumed to be equal. Cole let both equal unity (no mortality) in his original analysis.

Charnov and Schaffer also developed a model which incorporated delayed reproduction. The result (eq. [3]) was independent of prereproductive development time, but dependent on λ, the population growth rate.

$$\frac{B_S}{B_I} = \frac{1}{1 - P/\lambda},$$
(3)

where B_S = fecundity of the semelparous individual, B_I = yearly fecundity of the interoparous individual, and λ = population growth rate. In fact, equation (3) is identical to the result when equation (2) is presented as a relative, as opposed to absolute, difference in fecundity. For the annual population,

$$\lambda = B_S C.$$
(4)

Substituting for C in equation (2),

$$B_S = B_I + \frac{PB_S}{\lambda}$$

$$B_S - \frac{PB_S}{\lambda} = B_I$$

$$\frac{B_S}{B_I} = \frac{1}{1 - P/\lambda}.$$
(3)

Charnov and Schaffer are correct in stating that this result holds for all values of prereproductive development time. I will show later that this is true only if the time between reproductive episodes is held constant. This constraint will then be considered. Since λ is directly proportional to C (eq. [4]), their statements that increasing juvenile survivorship (eq. [2]) and increasing population growth rate (eq. [3]) favor semelparity are effectively equivalent.

The model I present below allows prereproductive development time, time between reproductive episodes, population growth rate, and adult survivorship to vary independently of one another, and incorporates senescence for the iteroparous life history. Senescence in this model is incorporated as the maximum number of reproductive episodes before death. By allowing this number to change from (1 to) 2 to infinity, an entire spectrum of iteroparous life histories can be examined. Semelparity may be considered an end point of this spectrum. The results of Cole and of Charnov and Schaffer will be shown to be special cases of this general model. Life history consequences will then be discussed.

THE MODEL

Consider a population consisting of two competing genotypes. One genotype is semelparous; the other is iteroparous. The environment in which they live determines juvenile survivorship and prereproductive development time (PDT hereafter), and these values are the same for both genotypes. In addition the environment determines adult survivorship, time between reproductive episodes

(TBR), and age of senescence for the iteroparous genotype. By *environment* I mean the shared genetic make-up of the two genotypes, and the shared biotic and abiotic surroundings which mold their phenotypes.

Both genotypes have a fixed and equal amount of resources available at the time of reproduction. The semelparous genotype devotes all of its resources to reproduction, and dies. The iteroparous genotype must divide its resources between reproduction and somatic growth and maintenance. The semelparous genotype will have a greater fecundity in its single reproductive episode, and the iteroparous genotype has some probability of surviving to reproduce again. This innate difference in fecundity is the degree to which the semelparous genotype is biologically capable of outproducing the iteroparous genotype in a given reproductive episode. This will be weighed against the difference in fecundity which is necessary for the two genotypes to have similar reproductive success.

In order for the semelparous genotype to be as reproductively successful as the iteroparous genotype, its fecundity must exceed the fecundity per episode of the iteroparous genotype. The degree of difference in fecundities necessary for equal reproductive success will depend, in part, upon the values of the life history traits listed above that are realized in a given environment. The less this necessary difference is, the more likely it is that the semelparous genotype can overcome it. The model below quantifies these relationships.

For the semelparous genotype,

$$\lambda_S^Y = C^Y B_S, \tag{5}$$

where λ_S = yearly population growth rate of the semelparous population, Y = prereproductive development time (PDT) in years, C = average yearly juvenile survivorship, and B_S = fecundity of a semelparous individual.

Yearly juvenile survivorship need not be constant, and the shape of the juvenile survivorship curve is not important. Total juvenile survivorship, C^Y, is the important value here. C^Y is the proportion of offspring produced which survive to reproductive age.

What is the fecundity per episode for the iteroparous genotype such that its yearly population growth rate is the same as that of the semelparous genotype? Let

a_t = number of adults alive at the beginning of year t;

b_t = number of offspring produced in year t;

λ_I = yearly population growth rate of the iteroparous genotype;

B_I = fecundity per episode of an iteroparous individual;

Z = time between reproductive episodes (TBR) in years;

$n = Y/Z$: the ratio of PDT to TBR;

P = average yearly adult survivorship; and

x = maximum number of reproductive episodes before senescence; all individuals surviving to reproduce x times die thereafter.

Juvenile survivorship and PDT are assumed to be the same for both the semelparous and the iteroparous genotypes. This assumption will be discussed later.

Let $\lambda_I = \lambda_S = \lambda$. Assuming a stable age distribution, all age classes are growing

AGE CLASS (numbers of individuals)

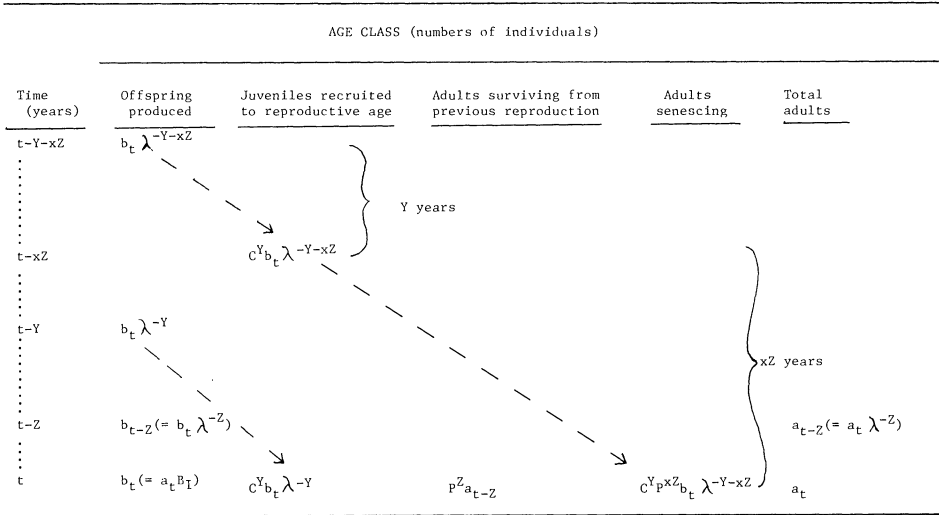| Time (years)	Offspring produced	Juveniles recruited to reproductive age	Adults surviving from previous reproduction	Adults senescing	Total adults
t-Y-xZ	$b_t \lambda^{-Y-xZ}$				
			} Y years		
t-xZ		$C^Y b_t \lambda^{-Y-xZ}$			
t-Y	$b_t \lambda^{-Y}$				
					} xZ years
t-Z	$b_{t-Z}(= b_t \lambda^{-Z})$				$a_{t-Z}(= a_t \lambda^{-Z})$
t	$b_t(= a_t B_I)$	$C^Y b_t \lambda^{-Y}$	$P^Z a_{t-Z}$	$C^Y P^{xZ} b_t \lambda^{-Y-xZ}$	a_t

Fig. 1.—Simplified life table for the iteroparous genotype showing the sources of recruitment for various age classes. Arrows indicate the progress of particular cohorts.

or declining at rate λ. Then $b_t \lambda^{-Y}$ = the number of offspring produced Y years ago, and $C^Y b_t \lambda^{-Y}$ = the number of those individuals surviving to reproductive age at time t. Also, $a_t \lambda^{-Z} = a_{t-Z}$ = the number of individuals alive at the previous reproductive episode, and $P^Z a_t \lambda^{-Z}$ = the number of those adults surviving to time t. Also, $b_t \lambda^{-Y-xZ}$ = the number of offspring produced $Y + xZ$ years ago, $C^Y b_t \lambda^{-Y-xZ}$ = the number of those individuals surviving to reproductive age, and $P^{xZ} C^Y b_t \lambda^{-Y-xZ}$ = the number of those individuals surviving to senescent age at time t. In addition,

$$B_I a_t = b_t;$$ (6)

the number of offspring produced at time t equals the number of adults alive at time t multiplied by their fecundity.

The total number of adults alive at time t equals the number of juveniles recruited to reproductive age plus the number of adults surviving from the previous reproductive episode less the number of adults senescing (eq. [7]):

$$a_t = C^Y b_t \lambda^{-Y} + P^Z a_t \lambda^{-Z} - P^{xZ} C^Y b_t \lambda^{-Y-xZ}.$$ (7)

This information is presented schematically in figure 1.

Substituting from equation (6), equation (7) becomes $1 = C^Y B_I \lambda^{-Y} + P^Z \lambda^{-Z} - C^Y B_1 \lambda^{-Y-xZ} P^{xZ}$. From equation (5), $C^Y = \lambda^Y / B_S$, so

$$1 = \frac{B_I}{B_S} + \left(\frac{P}{\lambda}\right)^Z - \frac{B_I}{B_S}\left(\frac{P}{\lambda}\right)^{xZ};$$

$$\frac{B_S}{B_I} = \frac{1 - (P/\lambda)^{xZ}}{1 - (P/\lambda)^Z} = \frac{1 - (P/\lambda)^{xY/n}}{1 - (P/\lambda)^{Y/n}}.$$ (8)

Equation (8) describes the relative difference in fecundity of semelparous and iteroparous life histories with equal population growth rates, given equal juvenile survivorships and developmental times and constant life-history values.

When $P/\lambda = 1$, equation (8) yields $B_S/B_I = 0/0$. Analysis shows that B_S/B_I equals x in this case and is independent of other life history traits (see Appendix A). When $x = 1$ or $P = 0$, $B_S/B_I = 1$. This represents the case where the "iteroparous" individuals die after first reproduction, making them semelparous. Aside from these special cases, the ratio B_S/B_I is greater than unity.

As stated earlier, the smaller the difference in fecundity, the more likely it is that the semelparous life history will be favored over the iteroparous life history. There are two ways to represent this difference in fecundity: relative and absolute. Equation (8) presents the general result as a relative difference, B_S/B_I. The absolute difference, $B_S - B_I$, can only be obtained expicitly when $(P/\lambda)^{xZ}$ approaches zero. If $x \to \infty$, then $P/\lambda < 1$, and $(P/\lambda)^{xZ} \to 0$ (see Appendix B). In this case of no senescence,

$$\frac{B_S}{B_I} = \frac{1}{1 - (P/\lambda)^{Y/n}}, \qquad (9)$$

the relative result with no senescence;

$$B_S - B_I = B_S(P/\lambda)^{Y/n};$$

$$B_S - B_I = (P/\lambda)^{Y/n}(\lambda/C)^Y. \qquad (10)$$

Equation (10) presents the general result as an absolute difference in fecundity. When $P = 0$, $B_S - B_I = 0$. Again this is the case where the "iteroparous" individuals are semelparous. Aside from this special case, $B_S - B_I$ is greater than zero.

Which quantity, B_S/B_I or $B_S - B_I$, is a more realistic measure of the difference in fecundity in the evolutionary sense? If the cost of iteroparity in terms of offspring not produced (to allow for continued adult survival) is proportional to fecundity, then the relative difference is appropriate. This may be the case where the entire organism must be maintained until the next reproduction, and fecundity is proportional to the size of the organism. If the cost of iteroparity is independent of fecundity, then the absolute difference is appropriate. This may be the case where future survival is limited to a given subset of the parent organism, such as an adventitious shoot, or fecundity is limited to a given amount independent of adult size.

Use of the relative or of the absolute difference in fecundity can lead to contradictory results, as will be shown below. All comparisons of relative and absolute differences below are for nonsenescent life histories ($x \to \infty$; $P/\lambda < 1$).

CASES AND CONSEQUENCES

The results of Cole (1954) and of Charnov and Schaffer (1973) are special cases of the general model. For the Charnov-Schaffer annual/perennial result (eq. [2]),

TABLE 1

NUMERICAL EXAMPLE IN WHICH RELATIVE DIFFERENCE DECREASES AND ABSOLUTE
DIFFERENCE INCREASES WITH THE SAME VALUES OF B_S AND B_I. NUMBERS CHOSEN
ARBITRARILY TO ILLUSTRATE THE PATTERN

	Small PDT	Large PDT	Δ
B_S	150	250	
B_I	50	100	
$B_S - B_I$	100	150	increases
B_S/B_I	3.0	2.5	decreases

let (a) $x \to \infty$, no senescence; (b) $Y = 1$, PDT $= 1$ yr; and $(c)n = 1$, TBR = PDT, 1 yr. Substituting into equation (10), $B_S - B_I = (P/Y) \cdot (Y/C)$, resulting in equation (2) $B_S - B_I = P/C$, from which follows Cole's result when $P/C = 1$.

As shown earlier, the Charnov-Schaffer result for delayed reproduction (eq. [3]) can be derived from their earlier result (eq. [2]). It is also a special case of equation (8). Let (d) $x \to \infty$, and (e) $Z = Y/n = 1$, TBR constant. Then

$$\frac{B_S}{B_I} = \frac{1 - (P/\lambda)^x}{1 - (P/\lambda)} = \frac{1}{1 - P/\lambda}. \tag{3}$$

The relative difference is independent of PDT, as stated by Charnov and Schaffer, if and only if TBR is held constant. In fact, TBR is not necessarily independent of PDT. For many animals and plants, TBR may be an increasing function of PDT. Such a relationship is well known for mammals; it has been documented intraspecifically for Atlantic salmon (Schaffer and Elson 1975) and the data of Waller (1979) provide evidence that it may hold for North American trees. This relationship is currently being analyzed for various living taxa. If TBR increases with increasing values of PDT, then the relative result (eq. [8]) is a decreasing function of PDT.

The absolute difference, $B_S - B_I$, has an entirely different relationship with PDT. Equation (10), with assumption d, becomes

$$B_S - B_1 = P/\lambda(\lambda/C)^Y. \tag{11}$$

This result is an increasing function of PDT for all $\lambda/C < 1$. $\lambda/C < 1$ iff $B_S > 1$. If assumption d is relaxed and TBR is allowed to increase with PDT, the result is still an increasing function of PDT as long as $P \geq C$.

Therefore, when the relative difference is considered, $B_S B_1$ is a nonincreasing function of PDT, and iteroparity is not favored by increasing values of PDT. When the absolute difference is considered, $B_S - B_I$ is usually an increasing function of PDT and iteroparity is favored by increasing values of PDT. Similar conclusions result when considering TBR.

These inconsistencies can be clarified by understanding that as PDT or TBR increases, fecundity must also increase if population growth rate is to be maintained. Therefore B_S/B_1 can decrease and $B_S = B_1$ can increase simultaneously (see table 1).
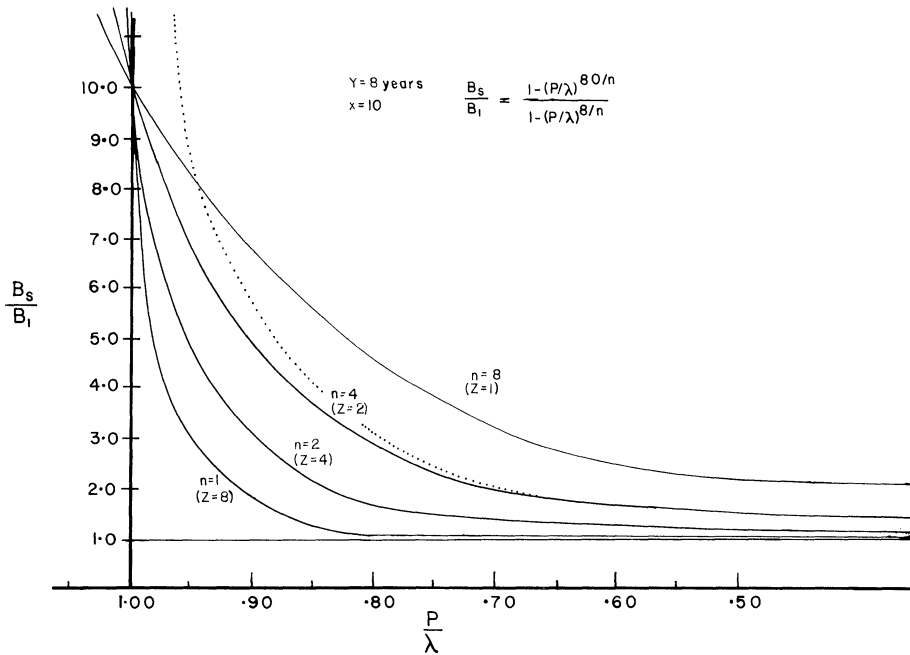
FIG. 2.—Change in the relative difference, B_S/B_I, with respect to P/λ and n. See text for explanation.

These results illustrate the necessity to explore the theoretical consequences and the biological plausibility of relative and absolute differences in fecundity. The two have been indiscriminately mixed in the past.

With respect to the remaining variables, P,C,λ, and n, both the relative and the absolute results behave qualitatively similarly. The addition of senescence (finite x) does not alter the direction of these trends with respect to the relative result. Increasing adult survivorship and age of senescence favor iteroparity. λ is generally an increasing function of C, and increasing values of both population growth rate and juvenile survivorship favor semelparity. Increasing values of n represent smaller values of TBR relative to PDT, and favor iteroparity.

Figure 2 shows how the relative difference in fecundity, B_S/B_1, behaves with respect to P/λ and n. PDT is fixed at 8 yr and x at 10 reproductive episodes. Each curve represents a given value of n (and TBR). The ordinate axis represents values of P/λ. A population growing at 5% per year with 80% adult survivorship has a P/λ value of .76. If the iteroparous genotype reproduces every 2 yr ($n = 4$), then semelparous-iteroparous reproductive equity is represented by the value $B_S/B_1 = 2.35$. This means that if the semelparous genotype can produce greater than 135% more offspring than the iteroparous genotype per episode, then semelparity will be favored. If less, then iteroparity will be favored. Similarly, a population with constant size adult survivorship of .95 ($P/\lambda = .95$) and a TBR of 8 yr has a value for equity of 2.90.

The dotted curve illustrates the effect of removing senescence from life histories

with $n = 4$. Two aspects of this curve are worth pointing out. First, the effect of senescence is slight at values of P/λ less than .85 and rapidly increases at greater values. Second, when there is no senescence, the value $P/\lambda = 1.00$ is asymptotic. This supports the conclusion of Appendix B, that when $x \to \infty$, then $P/\lambda < 1$.

The family of curves representing the different values of n may help to explain an interesting life-history phenomenon in the real world. In several taxa of rosette-producing plants with both semelparous and iteroparous representatives, the iteroparous species are found in the more mesic sites and the semelparous species are found in the drier, rockier sites (*Yucca-Agave,* Schaffer 1979; *Espeletia,* Smith 1980*a,* 1980*b*; *Lobelia spp.,* Young 1981). *Lobelia* rosettes invariably die after reproduction. Iteroparous individuals are those which produce multiple adventitious rosettes. The production of adventitious rosettes in drier sites may significantly reduce the suvivorship of the plant. In the *Yucca-Agave* system, the dry site agaves which do manage to produce innovative rosettes do so at the time of reproduction and death of the parent rosette. In addition, reproduction in these sites may occur more rarely as a result of low resource availability. These situations represent lesser values of n. Moist-site species may not be under these restrictions. Iteroparous lobelias produce innovative rosettes throughout their lives, independent of flowering time. Yuccas usually maintain the entire rosette after flowering. These situations represent greater values of n. The observed differences in life history may be a result of the fact that greater values of n favor iteroparity and lesser values favor semelparity. This does not preclude the possibility that other evolutionary forces may also be acting to select for the observed differences.

Assumptions Concerning the Juvenile Stage

Earlier it was assumed that yearly juvenile survivorships and development times were equal for the semelparous and iteroparous life histories. This assumption was made because, when considering the evolution of life histories, it is appropriate to consider the fate of two genotypes sharing one set of environmental constraints but differing with respect to a given life-history trait. Since the juvenile stage occurs prior to the critical difference between semelparity and iteroparity, it was assumed to be independent of this difference at the time the difference first evolves. There are at least two reasons why this may not be the case. First, an iteroparous individual may insure future survival by postponing reproduction instead of, or in addition to, reducing fecundity. This would mean an increased PDT for the iteroparous genotype. An alternative model could be produced which tests the difference in development times, rather than fecundities, as is done here. Second, survival of the adult may affect the survival of the juveniles, either positively or negatively. A detrimental effect would be a decreasing function of λ.

SUMMARY

Previous models of semelparity and iteroparity are critically reviewed. A general model is produced which incorporates population growth rate, juvenile and adult survivorship, prereproductive development time (PDT), time between repro-

ductive episodes (TBR), and senescence. Increasing values of population growth rate and juvenile survivorship favor semelparity. Increasing values of adult survivorship, age of senescence, and the ratio of PDT to TBR favor iteroparity. Ambiguities arise when analyzing the effect of PDT or TBR depending on whether an absolute or a relative difference in fecundity is considered. The biological implications of this and other aspects of the model are discussed.

APPENDIX A

$$B_S/B_I \quad \text{when } P = \lambda.$$

Equation (8) is constructed such that B_S/B_I cannot be correctly evaluated for $P = \lambda$. The following shows that $B_S/B_I = x$ in this case. From equation (5),

$$B_S = (\lambda/C)^Y.$$

From the characteristic equation,

$$1 = (C/\lambda)^Y B_I \left[1 + P/\lambda + (P/\lambda)^Z + (P/\lambda)^{2Z} + \ldots + (P/\lambda)^{(x-1)Z}\right]. \tag{A1}$$

When $P/\lambda = 1$,

$$(\lambda/C)^Y = B_I x. \tag{A2}$$

Therefore,

$$B_S/B_I = \frac{(\lambda/C)^Y}{(\lambda/C)^Y(1/x)} = x. \tag{A3}$$

This result is independent of other life-history parameters in this model (see fig. 2). All curves intersect the vertical axis $(P/\lambda = 1.00)$ at $B_S/B_I = 10.0$.

APPENDIX B

To show that if $x \to \infty$, then $P/\lambda < 1$, and therefore $[1 - (P/\lambda)^{xZ}] \to 1$. From equation (A1) in Appendix A,

$$B_I = \lambda^Y/C^Y[1 + P/\lambda + (P/\lambda)^Z + \ldots (P/\lambda)^{(x-1)Z}]^{-1}.$$

Assume the population has no senescence and $x \to \infty$. Then if the series $\Sigma_{Z=1}^{\infty} (P/\lambda)^Z$ does not converge, $B_I \to 0$. If the series does converge, then B_I can take on nonzero values. $\Sigma_{Z=1}^{\infty} 1(P/\lambda)^Z$ converges if $P/\lambda < 1$. Unless the population never reproduces, $P/\lambda < 1$ if $x \to \infty$. Therefore the term $[1 - (P/\lambda)^{xZ}]$ is equal to unity in reproductive populations with no senescence.

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