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Eric Charnov

William Schaffer

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LIFE-HISTORY CONSEQUENCES OF NATURAL SELECTION: COLE'S RESULT REVISITED

In his interesting paper on life-history strategies, Cole (1954) argued for the following result: "For an annual species, the absolute gain in intrinsic population growth that can be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one more individual to the average litter size." Thus, a clutch of size 101 at age 1 would serve the same purpose as having a clutch of size 100 every year forever. Gadgil and Bossert (1970) claimed that this was due to Cole's unrealistic assumption of no mortality during the life cycle, but Bryant (1971) proved the identical result with mortality present.

This again raises the question of why there should be perennials. In this note we shall prove some general results (of which Cole's and Bryant's are special cases) to give at least one answer to this.

Suppose we have two species, one an annual, the other a perennial. Both breed at the end of the first year and produce Ba and Bp offspring per individual, respectively. The proportion of offspring surviving the first year is C. Furthermore, the perennials have an adult survival rate of P per year.

If $N(T)$ is the number of organisms present in year T, counted just before reproduction but after the year's mortality, the rate of population growth (λ) is given by:

$$N(T+1) = \lambda \cdot N(T). \tag{1}$$

For the annual species:

$$N(T+1) = Ba \cdot C \cdot N(T) \quad \text{or} \quad \lambda a = Ba \cdot C. \tag{2}$$

For the perennial species:

$$N(T+1) = Bp \cdot C \cdot N(T) + P \cdot N(T)$$
$$= (Bp \cdot C + P) \cdot N(T) \tag{3}$$
$$\text{or} \quad \lambda p = Bp \cdot C + P.$$

If the populations are to increase at the same rate, $\lambda a = \lambda p$, or

$$Ba = Bp + P/C. \tag{4}$$

In Cole's case, $P = C = 1$; for Bryant, $P = C < 1$, which leads to the result:

$$Ba = Bp + 1. \tag{5}$$

[EDITOR'S NOTE: This letter derives from separate, similar contributions of the coauthors originally submitted at about the same time. The two authors were put into contact with each other, and the present contribution is a revised and extended version of their earlier efforts.]

Since $P >> C$ is more usual (see Deevey [1947] or Caughley [1966], for example), the evolution of perennial reproduction is much more likely. We therefore suggest that Cole's result be modified to read as follows.

"For an annual species, the absolute gain in intrinsic population growth rate that can be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding P/C individuals to the average litter size."

This suggests that the perennial habit should be favored in environments with low relative juvenile survival. It does not matter whether the mortality is density-dependent or independent, as long as it is age-specific, making P/C large.

Murphy (1968) has suggested a similar hypothesis for the more general situation of iteroparity and semelparity. While we are not prepared in this note to review arguments for the evolution of delayed reproduction, it is rather straightforward to generalize equation (4) to the case where the age of first reproduction is year K ($K > 1$). Let $C(K)$ be the immature survival rate, a nonincreasing function of K. The clutch size per individual for the semelparous species is Bs, and Bi for the iteroparous. P is the adult survival rate.

The characteristic equation for the iteroparous species is:

$$1 = Bi \cdot C(K) \left[1/\lambda^K + P/\lambda^{K+1} + P^2/\lambda^{K+2} + \ldots \right],$$

(6)

$$1 = \frac{Bi \cdot C(K)}{\lambda^K} \left[\frac{1}{1 - P/\lambda} \right].$$

For the semelparous species

$$1 = \frac{Bs \cdot C(K)}{\lambda^K} \quad \text{or} \quad \lambda^K = Bs \cdot C(K).$$

(7)

Substituting for λ^K in equation (6) we arrive at:

$$\frac{Bi}{Bs} = 1 - P/\lambda = R.$$

(8)

Iteroparity is favored by low R. This result depends on K only through λ; in that sense it is independent of K. Increasing K would often mean decreasing λ, which is the basis for Cole's claim that increasing the age of first reproduction favors iteroparity. At a fixed K, increasing juvenile mortality lowers λ, but does not affect P, thus again favoring iteroparity.

These simple models point to age specificity of the mortality factors in determining the optimal life-history pattern. Cody (1971) reaches identical conclusions from his review of bird reproduction.

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ERIC L. CHARNOV

ANIMAL RESOURCE ECOLOGY
  UNIVERSITY OF BRITISH COLUMBIA
    VANCOUVER 8, BRITISH COLUMBIA, CANADA

WILLIAM M. SCHAFFER

DEPARTMENT OF BIOLOGY
  UNIVERSITY OF UTAH
    SALT LAKE CITY, UTAH 84112
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