James Holland Jones [*,1,2]

[1]Department of Earth System Science, Stanford University,
[2]Woods Institute for the Environment, Stanford University

October 17, 2020

Videos

1   Introduction

When this paper was written, the dominant idea about life-history evolution came from MacArthur and Wilson (1967) in the form of r/K-selection theory. While MacArthur and Wilson originally stated the theory, it was Pianka (1970) who codified it into the form that persisted. This theory had a huge effect on the way anthropologists thought about the evolution of hominin life histories. Lovejoy (1981) famously used the theory to articulate his theory of the "demographic dilemma" that pair-bonding among the first hominins allegedly solved. r/K-selection theory was fatally flawed, as noted by Hairston et al. (1970) and then, devastatingly, by Stearns (1976).

In his introduction, Schaffer addresses the prediction from r/K-selection theory that more variable environments select for increased reproductive effort: "Both Cohen's results and those presented here suggest that generalizations common in the literature—namely, that fluctuating environments always favor greater reproduction, whereas constant environments always select for small litters and increased longevity (e.g., Pianka 1972)—are not deducible from theory." This is an idea that can be found in Lack (1947) and lots of other fundamental works on life-history patterns as well. As Schaffer notes, Cohen (1966) and Murphy (1968) both suggested that *age-specificity* in variation in mortality provided a better explanatory framework.

2   Schaffer's Model

Assume a *scalar* life history. All individuals are essentially identical. In effect, there is no age-structure. The fitness measure is the annual rate of increase, λ. B is annual production of

---

[*]Correspondence Address: Department of Earth System Science, Y2E2 Building, 473 Via Ortega, Room 140 Stanford, CA 94305-4216; phone: 650-721-2484, fax: 650-725-5099; email: `jhj1@stanford.edu`

daughters, what Schaffer calls "fecundity," and P be the annual post-breeding survival probability of adults. Note that B is in fact a composite parameter, reflecting both the mother's fertility and the survival of offspring to the census. It is clear that in this simple life history

$$\lambda = B + P \tag{1}$$

λ is the growth rate of the scalar population: $N_{t+1} = \lambda N_t$. Gadgil and Bossert (1970) noted that both B and P are likely to be functions of reproductive effort, denoted E by Schaffer (θ by Gadgil & Bossert).

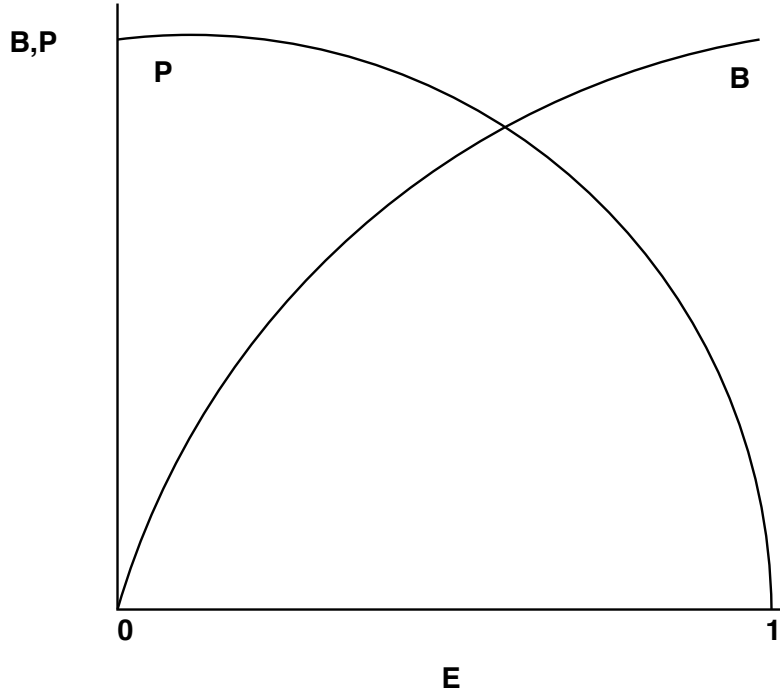

Figure 1: Fertility/Juvenile survival, B, and post-breeding survival, P, are functions of reproductive effort E

Fertility/juvenile survival increases with effort, whereas post-breeding survival decreases with effort. For concave[1] $P(E)$ and $B(E)$ (i.e., for diminishing returns to effort), the optimal life history lies at some intermediate point $0 \le E \le 1$, and the optimal reproductive effort, and hence life history, satisfies the relation

$$\frac{dB}{dE} = -\frac{dP}{dE}. \tag{2}$$

Optimal effort occurs where the marginal benefit of increased fertility associated with greater effort is exactly balanced by the marginal mortality cost. If both $P(E)$ and $B(E)$ are concave functions of E, then there will be an intermediate optimum.

---

[1]Note that Schaffer specifies what he means by "concave," namely $f''(E) < 0$, for a function of effort, $f(E)$.
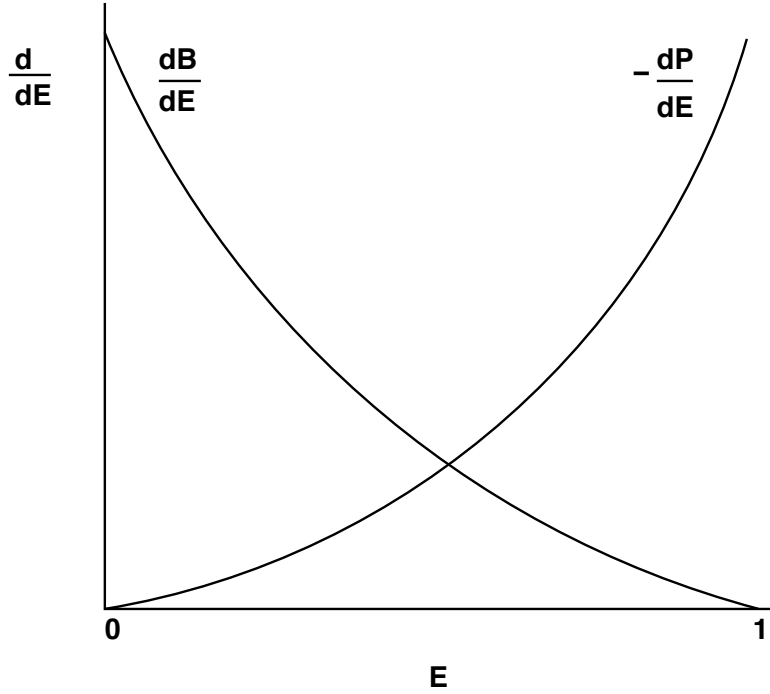
Figure 2: Optimal effort is where the marginal benefit of increased fecundity is balanced out by the marginal cost of effort on mortality.

When the environment is variable, the values of $B(E)$ and $P(E)$ will be different each year. Thus, λ will also vary by year. Given an initial population size N_0, the population size at time t will be

$$N_t = \lambda_{t-1}\lambda_{t-2}\dots\lambda_0 N_0.$$

The expected value of λ is:

$$\bar{\lambda} = \mathbb{E}\lambda(t) = \frac{1}{t}\lambda_{t-1}\lambda_{t-2}\dots\lambda_0,$$

and the expected population size at time t is then given by the following simplified relationship:

$$N_t = \bar{\lambda}^t N_0.$$

Clearly, fitness is maximized by maximizing $\bar{\lambda}$. While this statement is general, Schaffer analyzes a special case where there are two randomly distributed states: "good" and "bad." Because these states are randomly distributed and of equal frequency, Schaffer was able to focus on maximizing $\bar{\lambda}^2$ instead of $\bar{\lambda}$. Maximizing $\bar{\lambda}^2$ in the random-state environment is equivalent to maximizing $\bar{\lambda}$ because the square is a monotone transform. The two states have associated growth rates λ_g and λ_b respectively.

Denote the deviation from arithmetic mean fitness in good or bad years as s.

3

2.1   Case 1: Variation Affects Effective Fertility

Assume first that environmental fluctuations only affect the annual production of daughters. This could come about through reduced fertility of mothers or through reduced survival of immatures. In this case equation 1 for the two states becomes

$$\lambda_g = B(1+s) + P \tag{3}$$
$$\lambda_b = B(1-s) + P, \tag{4}$$

so that

$$\bar{\lambda}^2 = (B+P)^2 - s^2 B^2.$$

Assuming that both $B(E)$ and $P(E)$ are concave functions, then the optimal effort $\hat{E}$ satisfies the following relationship

$$\left(1 - \frac{s^2 B}{B+P}\right) \frac{dB}{dE} = -\frac{dP}{dE}. \tag{5}$$

The first term on the left-hand side of this equation is less than one. Thus, relative to the result for a constant population (equation 2), variation in fertility induces the optimal $\hat{E}$ to be inversely proportional to s. More variable environments for juvenile recruitment *favor reduced reproductive effort.*
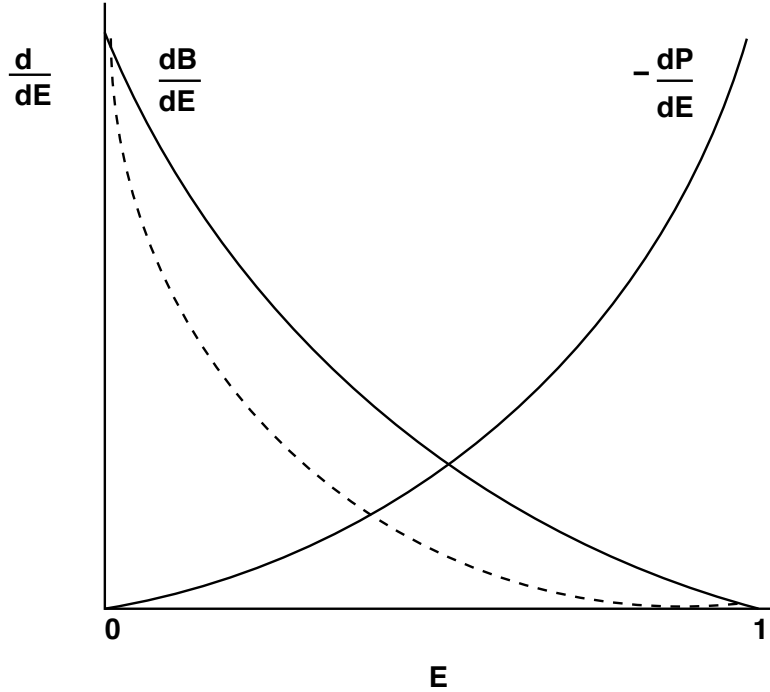

Figure 3: Variation in effective fertility favors reduced reproductive effort.

2.2 Case 2: Variation Affects Adult Survival

Now assume that environmental variability affects only post-breeding survival of adults, P.

$$\lambda_g = B + P(1+s) \qquad (6)$$
$$\lambda_b = B + P(1-s), \qquad (7)$$

so that

$$\bar{\lambda}^2 = (B+P)^2 - s^2 P^2.$$

Optimal E satisfies

$$\frac{dB}{dE} = -\left(1 - \frac{s^2 P}{B+P}\right)\frac{dP}{dE}. \qquad (8)$$

The first term on the right-hand side is less than one and the marginal fertility benefit to increased effort that balances the marginal survival cost is therefore lower. For variability affecting adult survival more variable environments for adult survival *favor greater reproductive effort*.
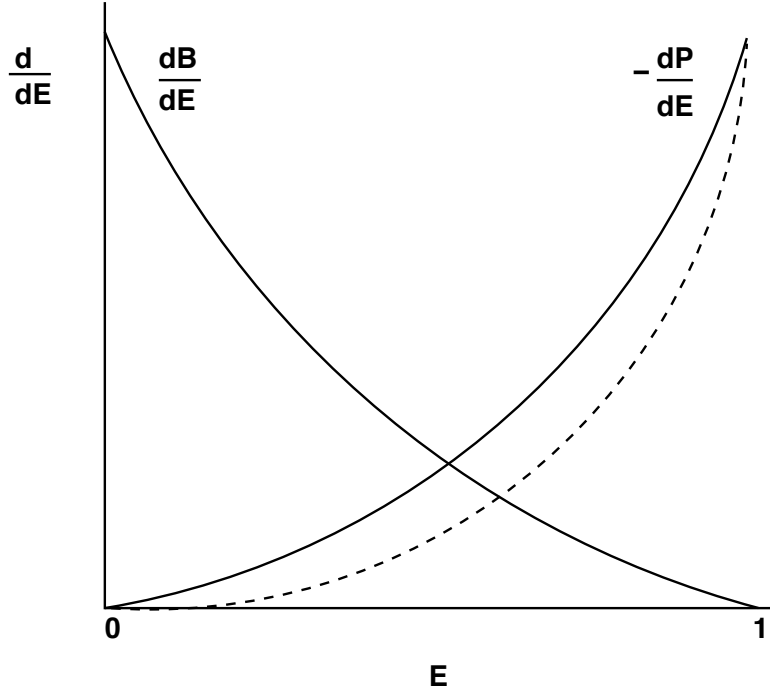

Figure 4: Variation in post-breeding survival favors increased reproductive effort.

References

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology 12* (1), 119–129.

Gadgil, M. and W. H. Bossert (1970). Life historical consequences of natural selection. *American Naturalist 104*, 1–24.

Hairston, N. G., D. W. Tinkle, and H. M. Wilbur (1970). Natural Selection and the Parameters of Population Growth. *The Journal of Wildlife Management 34* (4), 681–690.

Lack, D. (1947). The significance of clutch size. *Ibis 89* (2), 302–352.

Lovejoy, C. O. (1981). The Origin of Man. *Science 211* (4480), 341–350.

MacArthur, R. H. and E. O. Wilson (1967). *The theory of island biogeography*. Princeton: Princeton University Press.

Murphy, G. (1968). Pattern of life history and the environment. *American Naturalist 102*, 390–404.

Pianka, E. R. (1970). On r and K selection. *American Naturalist 104*, 592–597.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Quarterly Review of Biology 51* (1), 3–47.