

- . 1984. Cuticle: Ecological significance, pp. 685–693. In J. Bereiter-Haha, A. G. Matoltsy, and K. S. Richards (eds.), *Biology of the Integument*, Vol. 1—Invertebrates. Springer-Verlag, Heidelberg, W. Ger.
- JALLON, J., AND J. R. DAVID. 1987. Variations in cuticular hydrocarbons among the eight species of the *Drosophila melanogaster* subgroup. *Evolution* 41:294–302.
- KOISUMI, K. 1957. Antifungal action of cuticular lipids in insects. *J. Insect Physiol.* 1:40–51.
- MARKOW, T. A., R. C. RICHMOND, L. MUELLER, I. SHEER, S. ROMAN, C. LAETZ, AND L. LORENZ. 1980. Testing for rare male advantages among various *Drosophila melanogaster* genotypes. *Genet. Res.* 35: 59–64.
- PARTRIDGE, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. *Nature* 283: 290–291.
- PARTRIDGE, L., AND A. GARDNER. 1983. Failure to replicate the results of an experiment on the rare male effect in *Drosophila melanogaster*. *Amer. Natur.* 122:422–427.
- POMONIS, J. G., AND J. MACKLEY. 1985. Gas chromatographic composition profiles of surface lipid extracts from screwworm compared by age, sex, colonization and geography. *Southwest. Entomol.* 10:65–76.
- SCHAEFFER, S. W., C. J. BROWN, AND W. W. ANDERSON. 1984. Does mate choice affect fitness? *Genetics* 107:594.
- TAYLOR, C. E., A. D. PEREDA, AND J. A. FERRARI. 1987. On the correlation between mating success and offspring quality in *Drosophila melanogaster*. *Amer. Natur.* 129:721–729.
- TOOLSON, E. C. 1982. Effects of rearing temperature on cuticle permeability and epicuticular lipid composition in *Drosophila pseudoobscura*. *J. Exp. Zool.* 222:249–253.
- . 1984. Interindividual variation in epicuticular hydrocarbon composition and water loss rates of the cicada *Tibicen dealbatus* (Homoptera: Cicadidae). *Physiol. Zool.* 57:550–556.
- . 1988. Cuticular permeability and epicuticular hydrocarbon composition of Sonoran Desert *Drosophila pseudoobscura*, pp. 505–510. In F. Schnal, A. Zabza, and D. L. Denlinger (eds.), *Endocrinological Frontiers in Insect Physiological Ecology*. Wroclaw Technical Univ. Press, Wroclaw, Poland.
- TOOLSON, E. C., AND N. F. HADLEY. 1977. Cuticular permeability and epicuticular lipid composition in two Arizona Vejovid scorpions. *Physiol. Zool.* 50: 323–330.
- TOOLSON, E. C., AND N. F. HADLEY. 1979. Seasonal effects on cuticular permeability and epicuticular lipid composition in *Centruroides sculpturatus* Ewing 1928 (Scorpiones: Buthidae). *J. Comp. Physiol.* 129:319–325.

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THE EVOLUTION OF PHENOTYPIC VARIANCE WITH ITEROPARITY

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Bull (1987) examined the evolution of phenotypic variance and showed that random phenotypic variation can be favored in temporally varying environments. For the case of continuous phenotypic variation, Bull showed the optimal phenotypic variance is linearly and positively related to temporal environmental variance in the optimum phenotype and linearly and negatively related to the strength of stabilizing selection on the phenotype. This result generalized a number of other models of the evolution of variance in specific phenotypes (Cohen, 1966; Slatkin and Lande, 1976; Gillespie, 1977; Kaplan and Cooper, 1984), and it supports a large body of intuition and opinion on the adaptive value of phenotypic variance among siblings or within populations (Capinera, 1979; Crump, 1981; Kaplan and Cooper, 1984).

Bull's (1987) analysis of the evolution of phenotypic

variance did not consider the effect of other components of an organism's phenotype that decrease the chance of low fitness values. The most commonly suggested strategy for responding to variance in fitness across time periods is repeated reproduction over periods of time longer than the time scale of environmental variation (Schaffer, 1974; Goodman, 1984; Bulmer, 1985). By spreading progeny production over a broader time span, iteroparity can reduce the realized magnitude of environmental variation affecting offspring success. Can iteroparity thus reduce selection for phenotypic variation in a temporally varying environment? Here, I present a model that allows the evolution of phenotypic variance to be examined in a life-history context, and I examine the effect of iteroparity on the evolution of phenotypic variance.

The Model

Following Bull (1987), let the fitness of a newborn individual in generation t be a Gaussian function of its phenotype x , and of the environment ψ :

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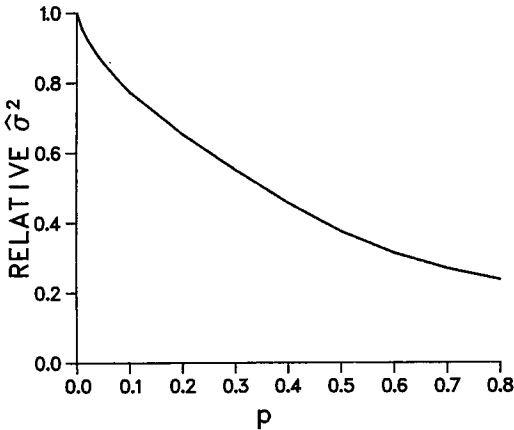


FIG. 1. The effect of increasing parental survival on the optimal phenotypic variance relative to the case of no contribution of parental survival to offspring success. The ordinate is the optimal phenotypic variance for an organism with overlapping generations expressed relative to that of an organism with nonoverlapping generations. The relative effect of parental survival is independent of the magnitude of environmental variation.

$$s(x, \psi) = c \exp\left\{-\frac{(x - \psi)^2}{2\omega^2}\right\}$$

where ψ_t is a measure of the environment in generation t expressed in terms of the phenotype that is optimally adapted to it, ω^2 is the strength of stabilizing selection, with small values representing strong stabilizing selection (equivalently, ω^2 can also be thought of as a measure of the environmental scope or tolerance of the phenotype, with large values representing broad environmental tolerance [Lynch and Gabriel, 1987]), and c is a constant equal to the maximum fitness of a phenotype in an environment to which it is optimally adapted. I assume that c is independent of genotype; all phenotypes have the same fitness in the environment to which they are optimally adapted.

In addition, if each genotype, k , has variable expression according to a normal density function $\phi(x|k)$, with mean μ and variance σ^2 , then total offspring success of an asexual genotype with nonoverlapping generations in an environment of type ψ_t is the integral of the product of the two above distributions multiplied by the total number of offspring produced, N :

$$b(k, \psi_t) = N \int_{-\infty}^{\infty} \phi(x|k) \cdot s(x, \psi_t) dx \quad (2)$$

$$b(k, \psi_t) = \frac{Nc\omega}{\sqrt{\sigma^2 + \omega^2}} \exp\left\{-\frac{\Delta^2}{2(\sigma^2 + \omega^2)}\right\} \quad (3)$$

where Δ is $\mu(k) - \psi_t$ (after Bull [1987]).

The fitness of an organism with nonoverlapping generations at time t is $b(k, \psi_t)$. However, for an iteroparous organism with overlapping generations, the expected representation in subsequent time periods must also include the probability of parental survival. Thus, fitness of an iteroparous organism is

$$w(k, \psi_t) = b(k, \psi_t) + p(t) \quad (4)$$

While $p(t)$ may be influenced by the environment, I suspect that in most cases this quantity will be influenced much less by extreme environments than will offspring success. So, for simplicity, I assume that $p(t)$ is independent of the environment and the genotype, and henceforth I use p for $p(t)$.

With temporal variation in the environment, the expected representation of genotype k over the long term is the geometric mean of the fitness over all ψ_t :

$$\bar{w}(k, \psi_t) = \prod_{\psi_t} [b(k, \psi_t) + p]^{\rho(\psi_t)} \quad (5)$$

where $\rho(\psi_t)$ is the probability of occurrence of environment ψ_t (Karlin and Liberman, 1974). Henceforth, I call variance in ψ_t "environmental variance."

In order to determine the importance of parental survival to the evolution of phenotypic variance, I performed a series of computer searches for maxima of Equation (5) with respect to σ^2 over a range of values of p and environmental variance. A hill-climbing algorithm was used to estimate $\hat{\sigma}^2$. For all searches, environmental variance was modeled as a normally distributed function, the mean phenotype $\mu(k)$ was assumed to equal the mean value of ψ_t , and the geometric mean fitness was constrained to 1, implying that, over the long term, the population size was stable. These searches revealed that $\hat{\sigma}^2$ increases with variance in ψ_t in a linear fashion, as in the case of nonoverlapping generations, but the slope of the relationship between $\hat{\sigma}^2$ and variance in ψ_t decreases as the contribution of parental survival to the geometric mean fitness increases. The relative decrease in the optimal phenotypic variance with increasing contribution of parental survival to geometric mean fitness is constant across all magnitudes of environmental variation and is shown in Figure 1. The introduction of a small amount of parental survival has a dramatic effect on the optimal phenotypic variance. A change in p from 0 to 0.01 decreases the optimal phenotypic variance 5%, relative to the case of nonoverlapping generations. When parental survival contributes only 0.1 to the geometric mean fitness ($p = 0.1$) the optimal phenotypic variance is decreased 23%, relative to the optimal phenotypic variance when there is no parental survival.

While this analysis treats parental survival as the variable of importance, the same analysis can be used to examine the importance of total offspring success on $\hat{\sigma}^2$. Change in offspring success that is uncorrelated with environmental variance may come about through change in the expectation of survival of individual offspring or through change in the absolute number of offspring produced. Change in total offspring success results in a change in the relative contribution of parental survival to geometric mean fitness of opposite sign. Thus, change in total offspring success and change in parental survival have opposite effects on $\hat{\sigma}^2$. The dependence of $\hat{\sigma}^2$ on total offspring success differs from the case of nonoverlapping generations.

DISCUSSION

It is clear from the analysis presented above that the introduction of parental survival and reproduction in more than one time period to a life history can strongly

reduce selection for phenotypic variance. This result is due to the buffering of fitness against very low values by parental survival. When parental survival is possible, selection favors genotypes that produce a relatively narrow range of phenotypes; a range suited for the more commonly occurring class of environments, rather than a range of phenotypes suited for the full range of environmental possibilities. An iteroparous strategy results in higher fitness in commonly encountered environmental situations and avoids very low fitness in rarely encountered environmental situations.

The general conclusion that can be drawn from the above analysis is that temporal environmental variation can select for an increase in phenotypic variation as Bull (1987) concluded, but the opportunity for repeated reproduction over a time scale longer than the scale of variation in the environment can lead to a significant reduction in the optimal phenotypic variance. Several specific predictions can also be made. First, we should expect, given similar measures of environmental variance, that semelparous or short-lived organisms will show greater phenotypic variation than will iteroparous and longer-lived organisms. Silvertown (1985) gives data on variation in seed morphology among annual and longer-lived species of the genus *Crepis* that agree with this prediction. Second, we should expect the difference in phenotypic variance between iteroparous and semelparous organisms to be greatest, on an absolute scale, when environmental variation is greatest. Third, among individuals within populations, or between years within populations, phenotypic variance should be positively correlated with fecundity.

Both Bull (1987) and I assume that there is no energetic cost associated with increasing phenotypic variance. Such variance might well be the result of random developmental noise and carry little or no cost. However, this assumption may be incorrect in many cases. Cost may be incurred through the regulation of the expression of progeny phenotypes or through differential investment in progeny. Asynchrony in ripening time of fruits in species with animal-dispersed seeds may result from selection imposed by variability in the time of arrival of dispersers (Smythe, 1970; McDonnell et al., 1984). Gorchov (1985) has shown that seed number per fruit is the likely proximate agent controlling ripening time in *Amelanchier arborea* and *Vaccinium corymbosum*. In each of these species, it appears that total seed production could be increased through an increase in the average number of seeds per fruit, but this would result in a more uniform ripening time (Gorchov, pers. comm.). Thus, phenotypic variation in ripening time in these species is more costly than simple developmental noise. With such costs associated with phenotypic variance, we might expect that the effectiveness of alternative means of adaptation, such as iteroparity, will be increased.

The results presented here support the conclusion of Bull (1987), and the suggestion of others (Capinera, 1979; Crump, 1981; Kaplan and Cooper, 1984) that environmental variation can select for phenotypic variation. However, these results point out that other aspects of the life history of the organism can buffer the effects of environmental variance and decrease the magnitude of selection for phenotypic variance in temporally varying environments.

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LITERATURE CITED

- BULL, J. J. 1987. The evolution of phenotypic variance. *Evolution* 41:303-315.
- BULMER, M. G. 1985. Selection for iteroparity in a variable environment. *Amer. Natur.* 126:63-71.
- CAPINERA, J. L. 1979. Qualitative variation in plants and insects: Effect of propagule size on ecological plasticity. *Amer. Natur.* 114:350-361.
- COHEN, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* 12: 119-129.
- CRUMP, M. L. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. *Amer. Natur.* 117:724-737.
- GILLESPIE, J. H. 1977. Natural selection for variance in offspring numbers: A new evolutionary principle. *Amer. Natur.* 111:1010-1014.
- GOODMAN, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. *Theoret. Popul. Biol.* 25:1-20.
- GORCHOV, D. 1985. Fruit ripening asynchrony is related to variable seed number in *Amelanchier* and *Vaccinium*. *Amer. J. Bot.* 72:1939-1943.
- KAPLAN, R. H., AND W. S. COOPER. 1984. The evolution of developmental plasticity in reproductive characteristics: An application of the "adaptive coin-flipping" principle. *Amer. Natur.* 123:393-410.
- KARLIN, S., AND U. LIBERMAN. 1974. Random temporal variation in selection intensities: Case of large population size. *Theoret. Popul. Biol.* 6:355-382.
- LYNCH, M., AND W. GABRIEL. 1987. Environmental tolerance. *Amer. Natur.* 129:283-303.
- MCDONNELL, M. J., E. W. STILES, G. P. CHEPLICK, AND J. J. ARMESTO. 1984. Bird-dispersal of *Phytolacca americana* L. and the influence of fruit removal on subsequent fruit development. *Amer. J. Bot.* 71: 895-901.
- SCHAFFER, W. M. 1974. Optimal reproductive effort in fluctuating environments. *Amer. Natur.* 108:783-790.
- SILVERTOWN, J. 1985. When plants play the field, pp. 143-153. *In* P. J. Greenwood, P. H. Harvey, and M. Slatkin (eds.), *Evolution: Essays in Honour of John Maynard Smith*. Cambridge Univ. Press, Cambridge, U.K.
- SLATKIN, M., AND R. LANDE. 1976. Niche width in a fluctuating environment—Density independent model. *Amer. Natur.* 110:31-55.
- SMYTHE, N. 1970. Neotropical fruiting seasons and seed dispersal. *Amer. Natur.* 104:25-35.