Variance Models in the Study of Life Histories

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VARIANCE MODELS IN THE STUDY OF LIFE HISTORIES

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Gillespie (1974) demonstrated mathematically that reducing the variance in offspring number could increase a genotype's fitness above that of another genotype having the same mean reproductive output. The implication was that natural selection could act upon the variance, as well as the mean of reproductive success, increased variance contributing negatively to fitness. Slatkin (1974) recognized the applicability of Gillespie's argument to the evolution of life histories and encouraged population ecologists to apply this idea to life history studies. Nichols et al. (1976) independently made a similar plea, suggesting that rather than represent the reproductive effort of a population as a point along an *r-K* continuum, it would be more appropriate to define effort as a frequency distribution. Consistent with this idea, Ekbohm et al. (1980) and Real (1980*a*, 1980*b*) added that an organism's fitness is likely to result from a trade-off between the mean and variance; many combinations of means and variances in fitness components can produce the same overall fitness.

Environmental variance has long been recognized as being important in determining evolutionary patterns (Bradshaw 1965; Levins 1968) as well as the evolution of life histories (Murphy 1968; Wilbur et al. 1974). Over 30 years ago, Skutch (1949) argued that selection favored larger mean clutch sizes in birds at high latitudes because larger clutches offset the increased variation in adult mortality. More recently, similar latitudinal trends in small mammals (Lord 1960), herbaceous Compositae (Levin and Turner 1977), and intralatitudinal studies of plants (Salisbury 1942) and birds (Moreau 1944) have also invoked environmental variability as an explanation for particular life history features. All of these organisms appear to have compensated for environmentally induced variance in survival by increasing the mean value of reproductive output. Environmental variance has also been posited as the explanation for the evolution of "bet-hedging" life histories (see Stearns 1976). Bet-hedging reduces the probability of extinction by temporally spacing individuals entering a life history stage, given that at certain unpredictable times a bad environment will result in zero survivorship or fecun-

dity at that stage. Thus, iteroparous organisms temporally space individuals entering the egg/seed stage, and many annual plants produce seeds with dormancy mechanisms that stagger their entrance into the vegetative stage.

While the above examples illustrate how environmental variability may be critical in life history evolution, the relationship of such environmental variability to variance in life history parameters is difficult to deduce. Variance occurs at both the environmental and life history levels, and we assume that the former is in some way related to the latter. The exact causative transition is difficult to make, however, because of the many spatial and temporal properties of environmental variability or heterogeneity (Levins 1968) and because environmental change can vary in intensity and occur at many different times in the life cycle of the organism (Stearns 1976). Correspondingly, variance in life history parameters may be intrinsic to the developmental patterns of the organism, environmentally induced or genetically determined. Difficulties in conceptualizing the role of variance may also be a consequence of the difficulty in assessing whether environmental heterogeneity, as perceived by us and our measuring instruments, is important for the organisms in question. A possibly more fruitful approach would be to use instead the organism's life history response as a measure of environmental heterogeneity (Clements and Goldsmith 1924; Hastings and Caswell 1979; Antonovics and Primack 1982). Finally, the problem of relating environmental variability to life history pattern may be the result of the absence of any theoretical (or empirical) framework for simultaneously considering the joint effects of means and variances on fitness. Here we attempt to provide such a framework. In particular we attempt to answer two questions. First, how can variance and mean be combined into a general and comprehensive model that can be applied to life history traits? Second, how can this mean-variance model then be deployed in empirical research?

THE MEAN-VARIANCE MODEL

The contribution that each trait makes to long-term or net fitness proceeds in a stepwise fashion. First the "trait" (x_i) will have a mean and variance that may independently affect the magnitude of one or several "fitness components" (f_j). Here we define a trait as any character measured on an organism, and by contrast, we define a fitness component as a character for which there is some a priori model describing how that character contributes to fitness. For example, the life history traits of age-specific survival and fecundity are considered fitness components, since they can be combined using the Euler equation to estimate future representation in the population (i.e., fitness). On the other hand, for a character such as leaf length, there is no a priori connection between the trait and future representation. The distinction between traits and fitness components will be largely operational, and somewhat arbitrary and tentative, but we make it here to emphasize the hierarchical generality of the models we present. The fitness components (e.g., survival, reproductive output, age to first reproduction) will in turn have a mean and variance that may independently determine "cohort fitness" (C), which we define as the contribution to the next generation of a group

of individuals uniquely defined both spatially and temporally. Each cohort will have a unique fitness value, depending on the spatial and temporal characteristics of the environment. Thus the distribution of fitnesses over cohorts will also have a mean and variance. These cohort differences can finally be combined over space and/or time to estimate "net fitness" (F). This term is used instead of long-term fitness to avoid the purely temporal (and somewhat indeterminate) connotation of the latter.

We now outline a general model for incorporating mean and variance values at the trait, fitness component, and cohort levels to estimate net fitness. Let x_i be the value of a trait i. The contribution of trait i to fitness component j we designate $f_{ij}(x_i)$. Our first step is to define and measure the expected value of the fitness component j in terms of a function H_{ij} of both the mean and the variance in trait i, e.g.,

$$E[f_{ij}(x_i)] = H_{ij}(\mu_i, \sigma_i^2)$$

where μ_i = mean value of the trait i and σ_i^2 = variance in trait i. Though the exact form of f_{ij} may be unknown, we can approximate it about μ_i by a Taylor's Series expansion:

$$f_{ij}(x_i) = f_{ij}(\mu_i) + f_{ij}'(\mu_i)(x_i - \mu_i) + \frac{f_{ij}''(\mu_i)}{2}(x_i - \mu_i)^2 + \ldots \quad (1)$$

Applying expected value operators to both sides of equation (1) yields:

$$E[f_{ij}(x_i)] = f_{ij}(\mu_i) + f_{ij}'(\mu_i)E(x_i - \mu_i) + \frac{f_{ij}''(\mu_i)}{2}E(x_i - \mu_i)^2 + \ldots \quad (2)$$

Noting that $E(x_i - \mu_i) = 0$ and that $E(x_i - \mu_i)^2$ equals the variance in the trait i (σ_i^2) we have

$$E[f_{ij}(x_i)] = f_{ij}(\mu_i) + \frac{1}{2}f_{ij}''(\mu_i)\sigma_i^2 + \ldots \quad (3)$$

Higher order terms in the Taylor's Series expansion similarly correspond to higher moments of the trait distribution, e.g., skew and kurtosis. Our mean-variance model ignores these higher terms, and provides an approximation for the expected value of fitness component j associated with trait i, which is a function solely of the trait mean and variance. This will be a close approximation for most biologically reasonable trait distributions (i.e., with finite moments). (The mathematically precise definition of "close approximation" is beyond the scope of this paper, but the utilitarian value of the approximation will be demonstrated in the data section.) The parameter $f_{ij}''(\mu_i)$ measures the curvature of f_{ij} at μ_i and expresses the sensitivity of the fitness component to variation in the trait. For example, a negative second derivative indicates that higher values of the trait show diminishing value in terms of the fitness component (fig. 1, curve A). This can be most clearly seen (fig. 2) if we assume trait i takes on either value A_i or B_i with equal probability. The expected value of the fitness component resulting
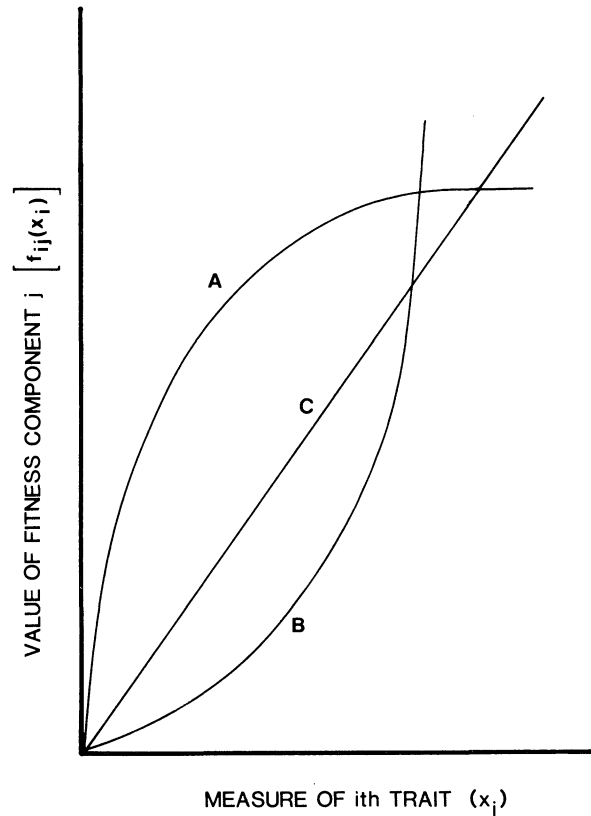
FIG. 1.—Some possible relationships between a fitness component j $[f_{ij}(x_i)]$ and values (x_i) for trait i. See text for further explanation.

from trait i is then given by the point where the chord between $f_{ij}(A_i)$ and $f_{ij}(B_i)$ crosses the mean value for the trait. If the mean value of the trait is held constant but the trait is allowed to assume higher or lower values, then the trait takes on either value A_i' or B_i'. The expected value of the fitness component under the new range is given by the chord between $f_{ij}(A_i')$ and $f_{ij}(B_i')$. For diminishing value $E[f_{ij}(x_i')] < E[f_{ij}(x_i)]$. A reduction in i below the mean produces a greater change in j than does a comparable increase above the mean.

Diminishing value of the fitness component is not, however, the only consequence of equation (3). The second derivative of f_{ij} could be positive (fig. 1, curve B) or zero (fig. 1, curve C). If it is positive, deviations above average are more advantageous evolutionarily than comparable deviations below average are disadvantageous. A zero second derivative for all values of x_i indicates no effect of variation on the fitness component; deviations in either direction are equally influential, and under these conditions the expected value is completely characterized by $f_{ij}(\mu_i)$. Real (1980b) presents a more extensive discussion of diminishing and accelerating fitness with biological examples.
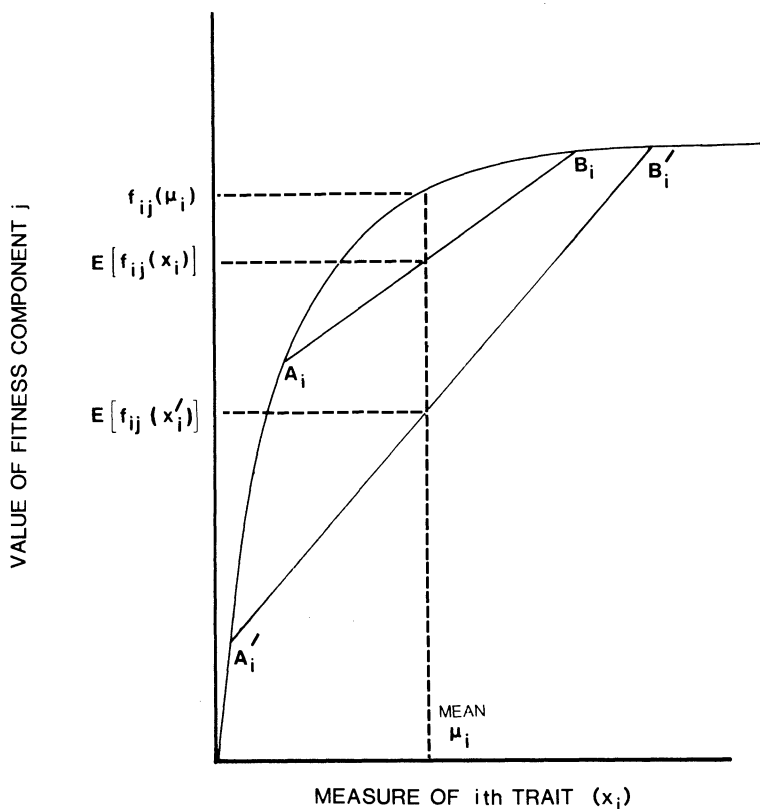
FIG. 2.—Value of the fitness component resulting from trait i, when the fitness relationship represents the diminishing contribution to fitness by increasing the value of trait i. The intersection of the chords ($A_i B_i$ and $A'_i B'_i$) with the trait mean show the expected value of the fitness component with different variances in trait i. See text for further explanation.

The expected value of the fitness component can be approximated by the value of f_{ij} at the mean discounted by a function of the trait variance:

$$E[f_{ij}(x_i)] \cong f_{ij}(\mu_i) + A_{ij}\sigma^2 \qquad (4)$$

where $A_{ij} = \frac{1}{2} [f''_{ij}(\mu_i)]$. The parameter A_{ij} has been called the "coefficient of risk" (Real 1980a, 1980b) and measures the degree to which j is influenced by variation in i (Lande 1980).

Any particular fitness component will undoubtedly be influenced by several traits, which may or may not contribute independently of each other. Let there be m traits that contribute to fitness component j, i.e., $f_j(x_1, x_2, \ldots, x_m)$. By an argument analogous to that for one trait, we can express the expected value of the fitness component by some combination of the expectation, variance, and covariance of the traits. Let X represent the vector of traits $(x_1, x_2, \ldots, x_m)$, and let $\bar{X}$ represent the vector of trait means $(\mu_1, \mu_2, \ldots, \mu_m)$. The fitness component

f_j is now a function of the trait vector X. The expected value of $f_j(X)$ approximated by a Taylor's Series expansion at the trait mean vector $\bar{X}$ is given by:

$$E\{f_j(X)\} = f_j(\bar{X}) + \tfrac{1}{2} \sum_{i=1}^{m} \frac{\partial^2 f_j(\bar{X})}{\partial^2 x_i}\sigma_i^2 + \sum_{i=1 \atop i \neq h}^{m} \sum_{h=1}^{m} \frac{\partial^2 f_j(\bar{X})}{\partial x_i \partial x_h}\sigma_{ih}$$

where σ_i^2 is the variance in trait i and σ_{ih} = covariance between traits h and i defined as the expected product of deviations of traits h and i from their respective means. A positive covariance indicates that the traits deviate in the same direction, and a negative covariance indicates that the traits deviate in opposite directions. The second and cross partials reveal the local curvature at the mean vector $\bar{X}$ in the directions of the respective trait variable. Negative second and cross partial derivatives represent risk aversion as in the single trait model. Selection will then operate to reduce the variance and positive covariance of traits. Covariance, however, unlike variance, can be negative. Thus, under risk aversion, increasing negative covariance would increase the expected value of the fitness component. If selection acts to reduce the variance in a fitness component, then selection should also favor negative covariance among traits that contribute positively to that particular component. For example, assume that seed set is positively correlated with plant height and leaf number but that plant height and leaf number negatively covary. When plant height falls below average, leaf number will be above average. This increase in leaf number will offset a decline in plant height and consequently reduce the variation in seed set.

Each cohort produces some set of fitness components that must be combined into a measure of fitness. Let C be a single-valued function of the fitness component vector $(f_1, f_2, \ldots, f_j)$. This function can take a specified or general form. For example, we may decide, a priori, that a function defining population growth rate (λ) would be appropriate. We can use the fitness components (age-specific survivorship and fecundity) to calculate λ by the Euler equation. Equivalently, we can specify λ as the dominant eigenvalue for the Leslie matrix constructed from the same fitness components. If no specified function seems suitable, we can use a generalized function that is similar to those we used at the trait level. Here again, we must consider the mean, variance, and covariance of the fitness components and the arguments for fitness components would be basically the same as those for traits.

The last level of our hierarchical model estimates net fitness, F, from a set of cohort fitnesses. Previous discussions of life history phenomena have provided us with some a priori methods for estimating net fitness. First, with nonoverlapping generations and no density dependence, Levins (1968) and MacArthur (1972) among others have stated that within-generation fitness of a genotype that is spread over a spatially heterogeneous environment is simply the summation of its fitnesses in each environment, i.e., arithmetic mean of cohort fitnesses. However, the arithmetic mean may overestimate the net growth rate if increasing growth rate shows constant diminishing returns, e.g., if density dependence acts most strongly in patches with the greatest growth rate (Venable and Lawlor 1980). Second, if the environment is spatially uniform but temporally heterogeneous, the

geometric mean fitness is more appropriate because contributions are multiplicative (Cohen 1966; Levins 1968; Schaffer 1974; Gillespie 1977). The geometric mean of the fitness distribution has been used to determine the outcome of selection in a number of models of gene frequency changes in heterogeneous environments (Haldane and Jayakar 1963; Karlin and Lieberman 1975; Ewens 1979; Roughgarden 1979). In a real world situation, whether the arithmetic or geometric mean is appropriate will depend in part on the scale of the heterogeneity. For example, if the scale is very large relative to the dispersal distance, the organism will experience in each generation a spatially heterogeneous environment that is not temporally variable; under such conditions the arithmetic mean may be more appropriate (Levins 1968; Venable and Lawlor 1980).

When environmental heterogeneity dictates the use of the geometric mean, we can still partition the effects of central tendency and variance in λ. The general form for net fitness using the geometric mean of λ is given by

$$F(\lambda) = e^{E(\log\lambda)}.$$

The net fitness $F(\lambda)$ can be approximated at the arithmetic mean of λ by:

$$F(\lambda) \cong \mu_\lambda - \frac{(\sigma_\lambda^2)}{2\mu_\lambda}$$

where μ_λ = the expectation of λ and σ_λ^2 = variance in λ (Young and Trent 1969). The net fitness is now divisible into the contributions from the arithmetic mean of λ and the variance in λ. The coefficient of risk is $-1/2\mu_\lambda$. The generalized method developed here therefore can be reconciled with the use of the geometric mean, as in more conventional approaches of discounting variance.

It also permits a further prediction: Increasing variance is always undesirable. Yet since the coefficient of risk declines as μ_λ increases, the sensitivity to variance in λ diminishes as the arithmetic mean increases. Biologically, the impact of a given level of variance on net fitness will be less if average cohort fitness is high. Populations characterized by unusually high growth rates should then show a lower reduction in fitness as a result of increased cohort variance in λ. We therefore expect variation in growth rate to be greater among "r-selected" species than among "K-selected" species because of this relaxed selection pressure.

EXPERIMENTAL EXAMPLES

We now address two further questions, What empirical evidence demonstrates the importance of mean and variance in fitness, and what experimental approaches permit us to translate the mean and variance of particular traits into cohort and net fitness? We discuss three examples: One that concerns yield variation in rice cultivars, *Oryza sativa;* one that concerns experimental populations of an annual weed, *Arabidopsis thaliana,* grown in a range of environments; and one that concerns the evolution of life history traits in natural populations of wild carrot, *Daucus carota.*

Oryza sativa.—If trait and fitness (or fitness-component) measures are available for a single genotype over a range of environments, it is possible to calculate the

relationship between the trait and fitness distributions in a straightforward manner. This approach is illustrated using long-term data on yield (the agronomic analogue of fitness) for four varieties of *Oryza sativa* grown repeatedly for many years at the Taichung Agricultural Experiment Station, Taiwan. Using polynomial regression (table 1), we see that many of the trait-yield combinations in these varieties (31/40) have a positive linear but negative quadratic component. Therefore, in a breeding program yield could be increased either by directional selection for an increase in the mean of the trait or by stabilizing selection for a decrease in its variance. The quadratic regression coefficient is equivalent to the curvature and hence is a direct measure of the coefficient of risk.

Arabidopsis thaliana.—In the above example, the effect of environmentally induced variance on fitness was predicted from the shape of the trait-fitness function. A more direct measure of the effect of variance on fitness can be obtained if a range of genotypes is each grown in a range of identical environments in a completely crossed design. Such experimental designs are commonly used in plant breeding programs to evaluate genotype × environment interactions (Yates and Cochran 1938; Perkins and Jinks 1968). Using these designs, one can evaluate the mean fitness or fitness component of each genotype over all environments, as well as environmentally induced mean and variance for any particular trait of that genotype. One can then ask if means and variances in a trait are correlated with different fitnesses.

This approach is illustrated using the data of Westerman (1971*a*, 1971*b*, 1971*c*) who grew inbred lines and reciprocal crosses of the annual *Arabidopsis thaliana* in a range of temperatures and photoperiods. Data for temperature regimes are based on 49 genotypes (7 parents and reciprocal F_1 crosses) in four temperatures; data for photoperiod are based on 36 genotypes (6 parents and reciprocal F_1 crosses) in three photoperiods. For each line or cross we calculated both the mean and variance of each trait over the range of a particular environmental regime. Standard multiple regression (Barr et al. 1976) of mean fruit number, which we used as a fitness component, on mean and variance showed that in several instances the variance of the trait significantly contributed to the value of the fitness component in addition to the contribution of the mean (table 2). Sometimes, increased fruit number is associated with a decrease in variance, indicating that decreased phenotypic variance would be favored. In other cases, however, increased phenotypic flexibility would be favored. Some examples are shown in figure 3. For temperature responses (figs. 3*a*, 3*b*), fruit number increases with a decrease in both mean and variance. In the photoperiod responses in which the mean is relatively more independent of the variance, fruit number increases with decreasing variance in flowering time (fig. 3*c*), but increases with increasing variance in plant height (fig. 3*d*).

In the above examples, we have asked questions about how environmentally induced variance in a trait may affect a fitness component of a particular genotype. However, individuals may not only show differences in their sensitivity to environmental effects, but may produce variable progeny. These variable progeny may be generated by sexual reproduction or may be generated by maternally induced and/or developmental events. Dimorphic fruits, temporal variance

TABLE 1

POLYNOMIAL REGRESSION OF YIELD OF BROWN RICE (kg/ha) AGAINST VARIOUS TRAITS IN DIFFERENT YEARS FOR SEVERAL RICE VARIETIES GROWN AT TAICHUNG EXPERIMENT STATION, TAIWAN

TYPE	VARIETY	Y_R	DAYS TO MATURITY		TILLER NO. (×10)		PANICLE NO. (×10)		HEIGHT		STRAW WT (×1)	KG/HA (×10^{-3})
			L	Q	L	Q	L	Q	L	Q	L	Q
Crop season I												
Taiwan native (ssp. *Indica*)	Pai-mi-fen	1943–1976	1465*	−9**	45	−.17	−59	.18	−50	.02	1.15	−.10
	Wu-chien	1930–1976	784*	−4**	−57*	.14*	6	−.01	12	−.01	1.31*	−.09*
Taiwan ponlai (ssp. *Japonica*)	Taichung-150	1943–1977	911	−5	13	−.02	41*	−.09	18	−.01	1.95	−.15
	Taichung-65	1930–1977	1076*	−6*	31***	−.05	34***	−.06	22**	−.01	.59	−.04
Crop season II												
Taiwan native (ssp. *Indica*)	Hsieh-lo	1946–1976	2221	−14	54	−.19	127	−.35	3	−.00	−.26	.03
	Shuang-chiang	1943–1976	442*	−4	14*	−.09	−95*	.25	−48	.02	−1.14	.09
Taiwan ponlai (ssp. *Japonica*)	Taichung-150	1942–1977	326*	−4	156	−.52	31	−.06	64*	−.03	2.23**	−.15
	Taichung-65	1930–1977	80	−1	55*	−.12	−71	.03	93**	−.04	−.42*	.09

NOTE.—The linear (L) and quadratic (Q) regression coefficients are shown; where the nonlinear effect was not significant, the significance level shown is for the linear effect alone: otherwise significances refer to both linear and quadratic coefficients. Data are untransformed; log-transformed data give only a few minor shifts in significance levels.

* $P < .05$.
** $P < .01$.
*** $P < .001$.

TABLE 2

RELATIONSHIP BETWEEN MEAN SILIQUE NUMBER (fitness component) AND MEAN AND VARIANCE OF
DIFFERENT TRAITS FOR LABORATORY AND WILD STRAINS OF *Arabidopsis* GROWN
UNDER A RANGE OF TEMPERATURES AND PHOTOPERIODS

Regime and Strain	Trait	Mean	Variance	R^2
TEMPERATURE				
Lab strains	Flowering time	−.28*	.15	.15
	Height	−.62***	−2.30***	.67
	Leaf no.	.59**	−1.62	.15
Wild strains	Flowering time	−.79***	−3.57*	.73
	Height	−1.00***	.18	.75
	Leaf no.	−.26**	2.92*	.68
PHOTOPERIOD				
Lab strains	Flowering time	−.62***	−.64***	.50
	Height	−.24*	3.10*	.51
	Leaf no.	1.17**	2.96	.25

NOTE.—Means and variances are calculated over environments within a genotype. All data are log-transformed.
* $P < .05$.
** $P < .01$.
*** $P < .001$.

in reproductive events, and effect of fruit position within inflorescence on seed size and number are examples of nonsegregational mechanisms for generating variable progeny. In both segregationally and nonsegregationally induced variance, the fitness of interest is the fitness of the progeny group.

If we heuristically consider the different genotypes in the *Arabidopsis* study to constitute a progeny group, we can illustrate the application of the variance discount concept to genotypically (as opposed to environmentally) induced variance. Thus we can ask whether progeny with higher or lower genetic variance would be favored, by analyzing how fruit number varies with the mean of a trait in a genotype, over the group of genotypes (table 3). In four cases, the quadratic components of the polynomial regressions are significantly negative (in only one case positive), indicating that fruit number of this genotypic group would increase if genetic variance in several traits were lower. The quadratic regression coefficients may in this case be considered "genotypic coefficients of risk," rather than "environmental coefficients of risk." Furthermore, we can ask whether in this situation, genetic and environmental variance are favored in similar ways by comparing the effect of environmental variance on fitness calculated in table 2 with the genotypic effect calculated from table 3. It can be seen that the values are often not congruent. This is most clearly so for leaf number in the wild strains under a range of temperatures, when the correlation of environmental variance in leaf number with fruit number is positive and significant, while the genotypic coefficient of risk is negative and significant. For leaf number, reduced genetic variance and increased environmental variance would be favored.

The experiment with *Arabidopsis* was carried out under highly controlled and artificial conditions; the results and interpretations should therefore be treated
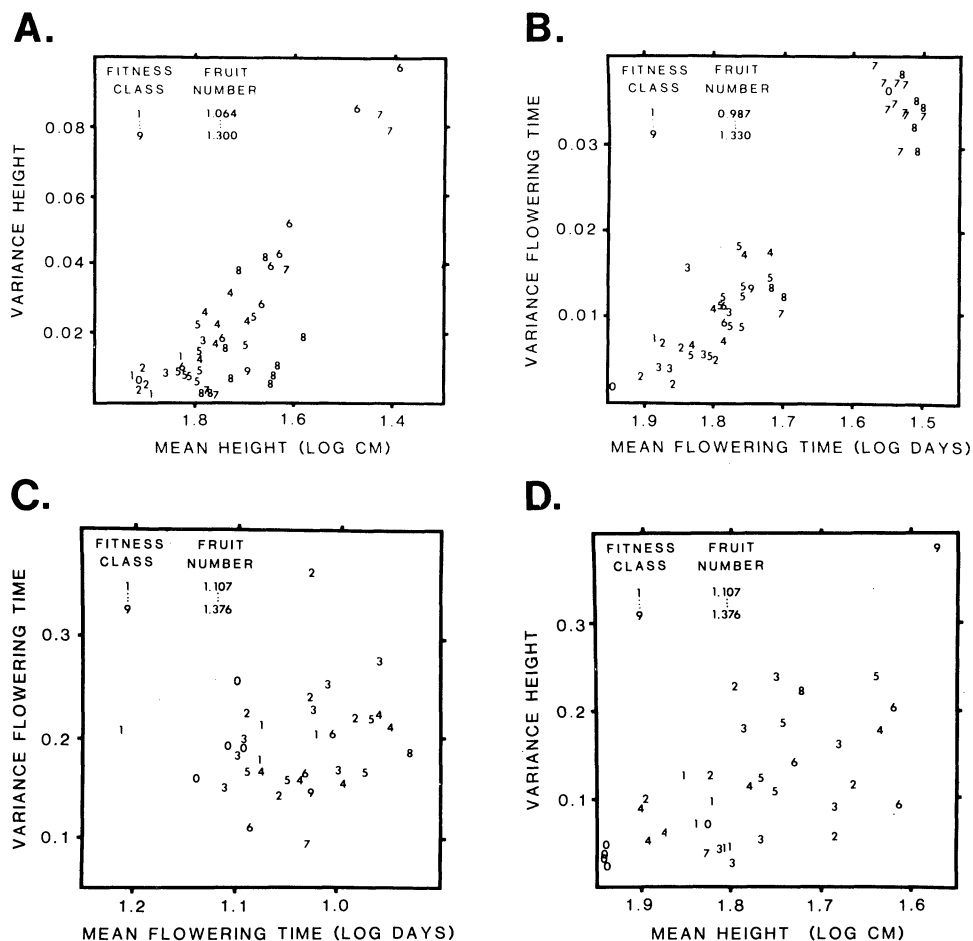
FIG. 3.—Relationship between fruit number and mean and variance of *A*, height of lab strains under a range of temperatures; *B*, flowering time of wild strains under a range of temperatures; *C*, flowering time of lab strains under a range of photoperiods; *D*, height of lab strains under a range of photoperiods. Each number = a different strain. Associated with each strain is a mean and variance for a character indicated by position on the graph, and a measure of the fitness component, fruit number, indicated by the value of number itself. This value represents 1 of 10 fitness classes (0–9) as indicated. Note that means have been scaled to correspond with increasing fitness along the abscissa. For statistical analysis of relationships among mean, variance, and fitness, see tables 2 and 3. Data from Westerman (1971*a*, 1971*b*). All data log-transformed.

TABLE 3

POLYNOMIAL REGRESSION OF MEAN SILIQUE NUMBER AGAINST VARIOUS TRAITS IN A RANGE OF
GENOTYPES FROM A DIALLEL CROSS, FOR SEVERAL STRAINS OF *Arabidopsis* GROWING
UNDER A SERIES OF TEMPERATURES AND PHOTOPERIODS

REGIME AND STRAIN	TRAIT	POLYNOMIAL REGRESSION COEFFICIENT	
		Linear	Quadratic
TEMPERATURE			
Lab strains	Flowering time	−16.97**	2.49**
	Height	8.57***	−1.20***
	Leaf no.	−18.60	3.05
Wild strains	Flowering time	11.61***	−1.64***
	Height	15.84	−2.25
	Leaf no.	9.47***	−1.58***
PHOTOPERIOD			
Lab strains	Flowering time	−1.73	.19
	Height	−2.11	.23
	Leaf no.	172.62*	−28.77*

NOTE.—All data log-transformed. Data from Westerman (1971*a*, 1971*b*, 1971*c*) where more experi-
mental details are described.
* $P < .05$.
** $P < .01$.
*** $P < .001$.

heuristically. They do not represent or attempt to mimic natural environments,
but the experimental design is straightforward and is readily transferable to a field
experiment (see Antonovics and Primack [1982] for an example).

Daucus carota.—In our third example we address the higher levels of our
hierarchical model by considering the integration of fitness components (f_j) and
cohort fitness values (C) to derive net fitness (F). We focus on the conditions
under which the biennial habit is favored over the annual habit in natural popula-
tions of *Daucus carota*. Biennials predominate in many populations of this
species, though within these populations some individuals may be annual, trien-
nial, or longer lived. These differences have a genetic component (E. Lacey,
personal observation). To compare the fitness of annuals and biennials, seeds
from natural populations were sown on freshly cleared plots for 3 yr. The fitness
components, germination, survivorship, and seed set, were measured on annuals
and biennials produced from each sowing. The data were then used to determine
cohort fitness using the Schaffer and Gadgil (1975) functions:

$$\lambda_A = cA \qquad \lambda_B = (cpB)^{1/2}$$

where λ_A = yearly population growth rate of annuals; λ_B = yearly growth rate of
biennials based upon geometric averaging; c = the probability of germinating and
surviving the first year; p = the probability that a first-year survivor survives
through the second year; A = the number of seeds produced by an annual; and B
= the number of seeds produced by a biennial.

There are several ways to calculate net fitness using these functions. Because

each sowing contained several plots that represented spatial variation within the field, we treated the seeds in each plot as a separate cohort and calculated λ for each plot (table 4). Then, because the variation in cohort fitness (among plots) was a spatial rather than temporal phenomenon, we arithmetically averaged the values of λ. Annuals showed a higher growth rate than biennials in two of the three sowings (table 5A). Because growth rates represent different points in time, we then used the geometric mean of the yearly growth rates to estimate net fitness. Under this situation, biennials showed a higher net fitness than annuals (table 5A).

Aside from the more general arguments supporting the various averaging methods, knowledge of the biology of the particular organism concerned is critical to our choosing a meaningful net fitness function. For example, in Michigan *D. carota* quickly colonizes recently abandoned fields (simulated by our experimental plots); however it can also persist in declining numbers for as long as 30 yr. Thus, when viewed over a number of fields that vary in age of abandonment (Lacey 1982), seedling and rosette survivorship in different fields represent not only spatial but also temporal variation (table 6). When we combine data from these different-aged populations with our experimental data, we also have across-field variation within years. In the absence of information about the organism's biology we would have arithmetically averaged these growth rates across fields. Because the fields constitute different stages in population growth and senescence (Holt 1972; Lacey 1982; Gross and Werner 1982), however, geometric averaging over cohorts is more reasonable. Therefore, for each year we also arithmetically determined the yearly growth rate within fields and geometrically averaged the growth rates over fields (table 5B). Using the geometric mean over years, we find that again the net fitness of biennials slightly surpasses that of annuals (table 5B). The geometric model is thus consistent with our empirical observations that *D. carota* is a "biennial" species in this geographical region and suggests that environmentally induced variance in cohort fitness enhances biennial over annual net fitness.

For the *D. carota* data, we have used only specified functions to estimate net fitness. We have not used a discount function for net fitness because we have no independent measure of net fitness. This lack of independence is a drawback not only of our data but of most empirical life history studies.

CONCLUSIONS

In modeling an organism's response to the environment, we find that variability may influence overall fitness in several ways. Variation may occur within individual traits that contribute to various fitness components; it may characterize the fitness components that determine cohort fitness; and it may arise when cohort fitnesses are combined to estimate net fitness. Our examples demonstrate that both mean and variance can contribute to fitness or its components and thereby influence evolutionary outcomes.

The contribution of mean and variance at each level to the success of different life history patterns can be determined empirically by growing genotypic classes in a series of environments in a crossed factorial design. This permits measure-

TABLE 4

FITNESS COMPONENT DATA FOR ANNUALS AND BIENNIALS OF *Daucus carota* IN EACH EXPERIMENTAL REPLICATE

EXPERIMENTAL PLOTS	GERMINATION	SURVIVORSHIP		SEED SET		λ	
		1st yr	2d yr	Annual	Biennial	Annual	Biennial
1976	.23	.23	.96	202(129)†	771(15)	10.69	6.26
	.39	.44	.57	202(129)†	771(15)	34.69	8.68
	.17	.78	.80	202(129)†	771(15)	26.78	9.04
	.33	.34	.83	202(129)†	771(15)	22.66	8.47
	.36	.37	.50	202(129)†	771(15)	26.91	7.17
1977	.33	.11	.79	0	1118(33)	0	5.66
	.31	.44	.81	0	1118(33)	0	11.11
	.27	.50	.76	0	1118(33)	0	10.71
	.29	.19	.78	44(4)	1118(33)	2.42	6.93
	.30	.46	.58	0	1118(33)	0	9.46
1979	.11	.65	.90	108(1)	680(2)	7.72	6.61
	.16	.72	.83	131(2)	168(2)	15.09	4.01
	.15	.40	.89	321(8)	2387(3)	19.26	11.29
	.24	.66	.90	290(7)	2136(2)	45.94	17.45
	.21	.67	1.00	163(8)	2079(5)	22.93	17.10
	.16	.52	.83	632(5)	1207(1)	52.58	9.13

NOTE.—The data come from seeds sown on freshly plowed plots at the Matthaei Botanical Gardens in Ann Arbor, Michigan. In 1976, 1,000 seeds per sample from each of two Michigan populations were scattered onto 1.0 × 0.5 m plots. In 1977 and 1979, sowings (500 sds/0.5 × 0.5 m) were repeated for three populations.

† (Sample size). When individual flowering plants were not kept separate by replicate, the mean seed set was calculated over all plants and was used for each replicate.

TABLE 5

YEARLY AND NET FITNESS OF ANNUALS (λA) AND BIENNIALS (λB) OF *Daucus carota*

	Year	λA	λB
		ARITHMETIC MEANS OVER PLOTS WITHIN YR	
A. Experimental plots only	1976	24.3	7.9
	1977	.5	8.8
	1979	27.3	10.9
Net fitness over years:			
Arithmetic mean		17.4	9.2
Geometric mean		6.9	9.1
		GEOMETRIC MEANS OVER FIELDS WITHIN YR	
B. Experimental and field plots	1976	3.6	2.9
	1977	1.1	6.2
	1979	27.3	10.9
Net fitness over years:			
Arithmetic mean		10.7	6.7
Geometric mean		4.8	5.8

NOTE.—Because we lack seed set data from natural populations, we have been constrained to use the experimental mean seed set values for all fields for each year. In (B) the experimental plots were treated as first year fields and combined with data from naturally occurring fields in 1976 and 1977. Data for 1979 are from experimental plots only.

TABLE 6

MEAN SURVIVORSHIP OF *Daucus carota* SEEDLINGS AND ROSETTES IN DIFFERENT-AGED FIELDS IN SOUTHEASTERN MICHIGAN

FIELD AGE (in yr since abandonment)	GERMINATION	SURVIVORSHIP			
		SEEDLINGS		ROSETTES	
		1976	1977	1976	1977
2	.28†	.10(1)††	...	.73(1)	...
2	.28	...	.07(2)	...	.95(2)
5	.28	.04(4)	...	.50(3)	...
7–9	.17	.29(4)	.42(3)	.52(3)	.95(3)
10–12	.17	...	.39(2)	...	.97(2)
>30	.17	.006(5)	.07(5)	.74(3)	.79(3)

† The germination values were extrapolated from Holt (1972), who sowed seeds into two different-aged fields.

†† (Sample size) = no. of plots for seedlings or transects for rosettes. One hundred rosettes were marked along each transect and seedling plots were set up at the ends of transects when seedlings were found.

ment of the effect of mean and variance on fitness directly and also permits further studies of the relationship between phenotypic plasticity (environmentally induced variance) and genetic variance in natural populations.

In life history studies a real difficulty with the empirical approaches that we have presented is that there is no independent measure of net fitness above and beyond the measured life history parameters themselves. The only viable solution is to estimate fitness independently by following populations through time and space. This has been done in population cage experiments with *Drosophila* (e.g., Prout 1969). Alternatively, seeds may simply be harvested and resown (i.e., nonoverlapping generations) as Suneson (1956) has done with multiple-cross mixtures. Estimates of genotype fitness have been obtained in this latter kind of experiment (Allard and Adams 1969). Studies of field populations are extremely difficult, however, because they require estimates of the time scale over which the changes have occurred as well as estimates of genetic variance and covariance of the traits. The greatest challenge is to obtain reliable estimates of net fitness of genotypes with contrasting life histories; it is clearly a challenge that may be met feasibly only in experimental systems, yet studies of such systems have barely been initiated.

The problems involved in accounting for variance in life history studies raise many more general issues about the circularity of evolutionary theorists, in this instance, theories of life history evolution. Given that models are mathematically correct, their falsifiability depends on the falsifiability of their explicit and implicit assumptions. If we use life history traits to measure fitness instead of measuring fitness independently (in long-term experiments, natural or man-made) it is clear that arguments about appropriate fitness functions will remain a scholastic exercise. It is perhaps time that, rather than bemoaning our inability to measure future fitness, we bite the bullet and measure, albeit over limited futures, future fitness.

SUMMARY

We propose a general model that estimates fitness from the joint effects of mean and variance. In this hierarchical model the contribution that each individual trait makes to net fitness proceeds in a stepwise fashion from the individual trait level to the fitness component and cohort fitness levels and, finally, to net fitness. We describe useful mathematical functions that incorporate both mean and variance values at each level. Empirical examples (1) demonstrate that variance, in addition to mean, can be an important determinant of fitness and (2) show how both can be used to estimate fitness, in particular in research addressing the evolution of life history patterns.

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