CHICAGO JOURNALS

Acquisition and Allocation of Resources: Genetic (CO) Variances, Selection, and Life Histories
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Source: *The American Naturalist*, Vol. 139, No. 4 (Apr., 1992), pp. 749-770
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2462620

ACQUISITION AND ALLOCATION OF RESOURCES: GENETIC (CO)VARIANCES, SELECTION, AND LIFE HISTORIES

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Submitted September 17, 1990; Revised April 29, 1991; Accepted June 6, 1991

Abstract.—We investigate a genetic model in which two traits result from the acquisition and allocation of a single resource. Phenotypic values for the two traits are written as a product of the total amount of the resource acquired and the proportion allotted to each of them. Although multiplicative gene action determines the traits, the epistasis at the gene level is mainly expressed in the additive genetic variance and covariance at the level of the measured traits. Phenotypic and additive genetic covariances between the two traits can be positive or negative; a negative additive genetic covariance can be accompanied by a positive phenotypic covariance. An acquisition-allocation model is the only model of multiplicative gene action that allows simultaneous selection on two traits to be written in matrix form. We use the model of resource acquisition and allocation to find the life-history consequences of acquisition of a resource and allocation to two traits. Two alternative allocation strategies—priority allocation to viability or to fecundity—lead to different evolutionarily stable strategies (ESSs) in life-history components. Primary allocation to fecundity has allocation fractions of zero or one as its stable state. Primary allocation to viability leads to an ESS allocation fraction that depends on resource availability, population growth rate, and the age structure of the population. In a poor environment and for inherently long-lived animals, the ESS allocation fraction tends in the direction of higher viability.

In life-history studies as well as in quantitative genetics, organisms are nearly always represented by a list of separate traits. Whereas the study of individual traits may be based on a physiological model of the ontogeny of the trait, the relations between traits are mostly studied as either phenotypic or genetic correlations without any consideration of the underlying physiology. Although the relations between life-history traits are usually thought to represent the result of alternative allocation of resources, explicit mechanistic models of this allocation process are rare. In quantitative genetics, correlated traits are assumed to result from pleiotropic gene action without any specification of how such pleiotropy comes about in the developmental pathways resulting in the traits.

Very often, the considerations are limited to the allocation of resources to competing goals without considering any variation in the acquisition of these resources. Allocation would lead one to expect a negative correlation between

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Am. Nat. 1992. Vol. 139, pp. 749–770.

the measurements of the competing traits, as Berenbaum et al. (1986) found between the amounts of two furanocoumarin derivates. Negative phenotypic correlations are not always found between life-history traits such as viability and fecundity (Smith 1981) or fecundity and longevity (Møller et al. 1989) that are a priori considered to form a trade-off. Occasionally, even a positive correlation has been found where a negative correlation had been expected (van Balen et al. 1987). As acquisition of a resource influences fitness components, we have in an earlier model (van Noordwijk and de Jong 1986) represented two traits as the product of the amount of a critical resource acquired and the fraction of this resource allocated to each trait. Depending on the relative variation in acquisition and in the allocation fraction, one obtains positive or negative phenotypic correlations between the traits. Here we elaborate on that model by considering the genetics of a two-level system, with one locus affecting the acquisition of the resource and a second locus affecting its allocation; that is, we present a version of the previous model with explicit genetic and environmental variation. We will consider not only the phenotypic variances and covariances of two traits determined by two such loci, but also the effect of selection pressure on those traits. The results of the two-locus model can be extrapolated to polygenic models.

An acquisition-allocation model is a translation of the idea of a trade-off in physiological terms. We give a direct genetic and quantitative genetic description, and we show the implications in terms of those fields. Trade-offs underlying life-history traits are real, whether they are formulated in very general terms, such as reproductive effort (Schaffer 1974*a*), in precise biochemical terms, such as the furanocoumarin skeleton as a precursor for several substances defending wild parsnip against the parsnip webworm (Berenbaum et al. 1986), or at any level in between, such as energy budgets in insects (de Ruiter and Ernsting 1987). Selection pressure on life-history strategies is a possible interpretation of the selection in the two-locus model. The translation from a formal selection model to a model of selection in life-history strategies can be done in more than one way. Two translations are found in the literature, but one is much more prevalent than the other. Our model shows this to be a consequence of differential preference by modelers. An acquisition-allocation model can be used to show the variety in the structure of life histories that is possible.

In this model the units of the two traits are the amounts of resource each trait receives, that is, the product of the total amount of resource acquired and the fraction allocated to each trait. It is usual to use a logarithmic transformation for quantitative traits that might arise from multiplicative processes in the estimation of heritabilities and genetic covariances. Here we chose not to transform, for four reasons. First, the traits as used represent amounts of resource: it seems biologically more accurate to work with amounts of resource throughout than with the sum of the logarithm of the total resource acquired and the logarithm of the fraction of the resource allocated to a trait. The units of the traits seem more consistent. Second, it is informative to know how multiplicative genetic models actually behave in quantitative genetics. Third, one does not always know whether a trait is additively or multiplicatively composed. Fourth, writing models of selection pressure on the traits while using the genetic variance of the log-

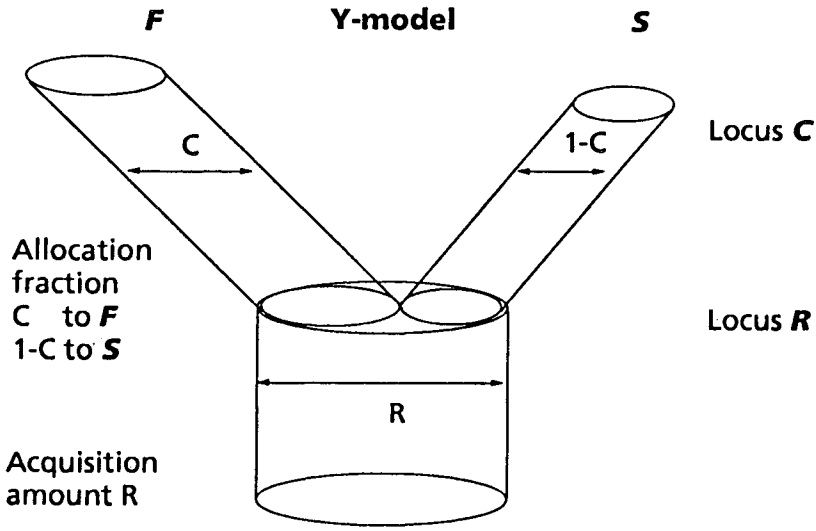

FIG. 1.—Diagram of the simplest Y model. An amount of resource acquired goes through the stem of the Y and is divided between the branches, leading to allocation of the resource acquired to the traits F and S.

transformed variables introduces the assumption that selection works on the log transformation of the traits. We chose to develop a model of selection pressure on the amounts of resource devoted to two traits related by a trade-off.

THE BASIC MODEL

The basic model consists of two traits F and S, arising from the allocation of a single resource (fig. 1). The traits F and S are measured in the units of the resource. Without any variation, a fraction, $C(0 < C < 1)$, of the amount of resource, $R(R > 1)$, will be actively allocated to F, and the remaining fraction, $1 - C$, will by default be allocated to S (see Appendix A for notation, which is kept consistent with Falconer 1981). Trait values for F and for S are found multiplicatively: the trait value F for trait F would be RC and the trait value S for trait S would be $R(1 - C)$. The diagram in figure 1 makes it clear why it is easy to speak of a Y model.

Genetic variation is assumed in both the amount acquired and in the fraction allocated to F. One locus, R, affects the acquisition of the resource. This locus has two alleles, R_1 and R_2, with frequencies p and $q = 1 - p$; the genotypic values for the three genotypes are $R_{11} = R + r_{11}$, R_{12}, and $R_{22} = R + r_{22}$; we are not yet supposing additive gene action within the locus. Note that a common level of gene action, R, is explicitly introduced for the three genotypes. A second locus, C, affects the allocation, the fraction that goes to trait F, while the fraction that goes to trait S passively follows. Locus C has two alleles, C_1 and C_2, with frequencies u and $v = 1 - u$; the genotypic values are $C_{11} = C + c_{11}$, $C_{12} = C$

$+ c_{12}$, and $C_{22} = C + c_{22}$, in a notation analogous to the one for locus $\boldsymbol{R}$. The recombination fraction between the two loci is ξ. Linkage disequilibrium will be considered in Appendix B.

The values for the two traits $\boldsymbol{F}$ and $\boldsymbol{S}$ for a certain genotype $\boldsymbol{R}_i\boldsymbol{R}_j\boldsymbol{C}_k\boldsymbol{C}_l$ can be written as products of the genotypic values at $\boldsymbol{R}$ and $\boldsymbol{C}$:

$$F_{ijkl} = R_{ij}C_{kl} = (R + r_{ij})(C + c_{kl}) \tag{1a}$$

and

$$S_{ijkl} = R_{ij}(1 - C_{kl}) = (R + r_{ij})(1 - C - c_{kl}), \tag{1b}$$

where r_{ij} is defined by the expansion of the genotypic value $R_{ij} = R + r_{ij}$ and c_{kl} is the expansion of the genotypic value $C_{kl} = C + c_{kl}$.

The population means of the genotypic values per locus are written as $\overline{C}$ and $\overline{R}$. At linkage equilibrium, $\overline{F} = \overline{R}\,\overline{C}$ and $\overline{S} = \overline{R}(1 - \overline{C})$.

The average effect, ρ, of a gene substitution at locus $\boldsymbol{R}$ for the amount of resource acquired is given by $\frac{1}{2}\,\partial\overline{R}/\partial p = pr_{11} + (q - p)r_{12} - qr_{22}$, while the average effect of a gene substitution at locus $\boldsymbol{R}$ for trait $\boldsymbol{F}$ is given by $\frac{1}{2}\,\partial\overline{R}\,\overline{C}/\partial p = \rho\overline{C}$ and for trait $\boldsymbol{S}$ by $\frac{1}{2}\,\partial\overline{R}(1 - \overline{C})/\partial p = \rho(1 - \overline{C})$ (Kojima 1959). These formulations are compatible with the average effects of a gene substitution as found by summation (Kempthorne 1957). The dominance effect, d, at locus $\boldsymbol{R}$ for the amount of resource acquired is given by $d = -\frac{1}{2}\,\partial\rho/\partial p = -\frac{1}{4}\,\partial^2\overline{R}/\partial p^2 = r_{12} - \frac{1}{2}(r_{11} + r_{22})$ (Kojima 1959), while the dominance effect at locus $\boldsymbol{R}$ for trait $\boldsymbol{F}$ is given by $-\frac{1}{2}\,\partial\rho\overline{C}/\partial p = -\frac{1}{4}\,\partial^2\overline{R}\,\overline{C}/\partial p^2 = d\overline{C}$ and for trait $\boldsymbol{S}$ by $-\frac{1}{2}\,\partial\rho(1 - \overline{C})/\partial p = -\frac{1}{4}\,\partial^2\overline{R}(1 - \overline{C})/\partial p^2 = d(1 - \overline{C})$. The average effect, γ, of a gene substitution at locus $\boldsymbol{C}$ for allocation is given by $\gamma = \frac{1}{2}\,\partial\overline{C}/\partial u$; for trait $\boldsymbol{F}$, the average effect of a gene substitution at locus $\boldsymbol{C}$ is given by $\frac{1}{2}\,\partial\overline{R}\,\overline{C}/\partial u = \gamma\overline{R}$, but for trait $\boldsymbol{S}$ it is given by $\frac{1}{2}\,\partial\overline{R}(1 - \overline{C})/\partial u = -\gamma\overline{R}$; similarly, the dominance effect, e, at locus $\boldsymbol{C}$ for allocation is given by $e = c_{12} - \frac{1}{2}(c_{11} + c_{22})$ and by $e\overline{R}$ for trait $\boldsymbol{F}$, but by $-e\overline{R}$ for trait $\boldsymbol{S}$. For trait $\boldsymbol{F}$, the additive by additive interaction is related to $\partial^2\overline{R}\,\overline{C}/\partial p\,\partial u$ (Kojima 1959); the additive (locus $\boldsymbol{R}$) by dominance (locus $\boldsymbol{C}$) interaction is related to $\partial^3\overline{R}\,\overline{C}/\partial p\,\partial u^2$, the dominance (locus $\boldsymbol{R}$) by additive (locus $\boldsymbol{C}$) interaction is related to $\partial^3\overline{R}\,\overline{C}/\partial p^2\,\partial u$, and the dominance by dominance interaction is related to $\partial^4\overline{R}\,\overline{C}/\partial p^2\,\partial u^2$.

The within-locus additive genetic variance at locus $\boldsymbol{R}$ equals $2pq\rho^2$, the dominance variance $(2pqd)^2$; the within-locus additive genetic variance at locus $\boldsymbol{C}$ equals $2uv\gamma^2$, the dominance variance $(2uve)^2$.

Apart from the influence of the loci, there is an environmental error independently on acquisition (ϵ_R) and on allocation. The environmental error on allocation adds ϵ_C to the allocation to trait $\boldsymbol{F}$ and subtracts the same amount, ϵ_C, from the allocation to trait $\boldsymbol{S}$. These environmental errors are seen as noise and have a mean of zero. The variance of the environmental error on acquisition is σ_R^2; the variance of the environmental error on allocation is σ_C^2. The covariance between trait $\boldsymbol{F}$ and trait $\boldsymbol{S}$ in the environmental errors is σ_R^2 at the acquisition level and $-\sigma_C^2$ at the allocation level. The total variance at the acquisition level is $2pq\rho^2 + (2pqd)^2 + \sigma_R^2$; the total variance at the allocation level is $2uv\gamma^2 + (2uve)^2 + \sigma_C^2$, both for trait $\boldsymbol{F}$ and for trait $\boldsymbol{S}$. The covariance between trait $\boldsymbol{F}$ and trait $\boldsymbol{S}$ is

TABLE 1

TWO-LOCUS Y MODEL: PHENOTYPIC VARIANCE AND COVARIANCE FOR THE TRAITS F AND S

(Co)Variance	Formula
var(F)	$\bar{C}^2[2pq\rho^2 + (2pqd)^2 + \sigma_R^2]$ $+ \bar{R}^2[2uv\gamma^2 + (2uve)^2 + \sigma_C^2]$ $+ [2pq\rho^2 + (2pqd)^2 + \sigma_R^2][2uv\gamma^2 + (2uve)^2 + \sigma_C^2]$
var(S)	$(1 - \bar{C})^2[2pq\rho^2 + (2pqd)^2 + \sigma_R^2]$ $+ \bar{R}^2[2uv\gamma^2 + (2uve)^2 + \sigma_C^2]$ $+ [2pq\rho^2 + (2pqd)^2 + \sigma_R^2][2uv\gamma^2 + (2uve)^2 + \sigma_C^2]$
cov(F,S)	$(1 - \bar{C})^2 \cdot \bar{C}[2pq\rho^2 + (2pqd)^2 + \sigma_R^2]$ $- \bar{R}^2[2uv\gamma^2 + (2uve)^2 + \sigma_C^2]$ $+ [2pq\rho^2 + (2pqd)^2 + \sigma_R^2][-2uv\gamma^2 - (2uve)^2$ $- \sigma_C^2]$

$2pq\rho^2 + (2pqd)^2 + \sigma_R^2$ at the acquisition level and $-2uv\gamma^2 - (2uve)^2 - \sigma_C^2$ at the allocation level.

VARIANCE AND COVARIANCE

We want the phenotypic variances of the traits F and S and the decomposition of the phenotypic variances into additive genetic variance and other variance components. One can derive the phenotypic variances of the traits F and S from the variances of acquisition and allocation through the general expression for the variance of products of independent variables. The variance of a product xy, where x and y are independently distributed variables with means $\bar{x}$ and $\bar{y}$ and variances σ_x^2 and σ_y^2, respectively, is (Goodman 1980, 1982)

$$\text{var}(xy) = \bar{x}^2 \cdot \sigma_y^2 + \bar{y}^2 \cdot \sigma_x^2 + \sigma_x^2 \cdot \sigma_y^2, \tag{2a}$$

and the covariance of xy and $x(1 - y)$ is

$$\text{cov}(xy, x(1 - y)) = \bar{y} \cdot \sigma_x^2 - \text{var}(xy) = \bar{y}(1 - \bar{y}) \cdot \sigma_x^2 - \bar{x}^2 \cdot \sigma_y^2 - \sigma_x^2 \cdot \sigma_y^2 \tag{2b}$$

(Riska 1986; van Noordwijk and de Jong 1986; Brown 1988).

Applying these general forms to the phenotypic variance of the traits F and S and their covariance yields the quantities in table 1. The phenotypic covariance between F and S is not necessarily negative, despite the fact that the traits F and S originate in a trade-off. Whether due to genetic causes or environmental noise, a large variance at the acquisition level easily leads to a positive covariance between the trade-off traits (van Noordwijk and de Jong 1986).

As can be seen in table 1, the phenotypic variance of the traits F and S has both genetic and environmental causes. A comparison with variance components as they appear in quantitative genetics is possible. In quantitative genetics, the standard way of formally decomposing a trait is as P = G + E: the phenotype is made up of a genotypic and an environmental contribution that work additively.

The genotypic contribution can be split into the breeding value or additive genetic part, A, a dominance deviation, D, and a genetic interaction, I: G = A + D + I. The interaction can again be split, into additive by additive, additive by dominant, dominant by additive, and dominant by dominant interactions: I = AA + AD + DA + DD. Environmental by genetic interaction terms might also be introduced: AE, DE, and EE. The phenotypic variance (V_P) and the phenotypic covariance (COV_P) between two traits can therefore be subdivided into independent components due to a certain type of gene action and to the environment:

$$V_P = V_A + V_D + V_{AA} + V_{AD} + V_{DA} + V_{DD} + V_E + V_{AE} + V_{DE} + V_{EE} \quad (3a)$$

and

$$\begin{aligned} COV_P = {} & COV_A + COV_D + COV_{AA} + COV_{AD} + COV_{DA} + COV_{DD} \\ & + COV_E + COV_{AE} + COV_{DE} + COV_{EE}. \end{aligned} \quad (3b)$$

The additive genetic variance and dominance variance in the traits are found directly from the definitions of the average effect of a gene substitution and the dominance effect (Kempthorne 1957; Kojima 1959). The additive by additive interaction variance is found by the method given by Kojima (1959), and the additive by dominance, dominance by additive, and dominance by dominance variances are found by an extension of that method (see Basic Model). The variance and covariance components in table 2 are therefore found independently from, but show a clear relationship to, the phenotypic (co)variance in table 1. At the genetic level, the genotypic values for the traits are found by multiplication of the per locus genotypic values, but this contributes not so much to the interaction variance as to the additive genetic variance. In the additive genetic variance of a trait, the additive genetic variance at one locus is multiplied by the square of the mean genotypic value at the other locus. Epistasis at the genetic level therefore contributes strongly to the additive genetic variance. Similarly, epistasis at the genetic level contributes to the dominance variance. The additive by additive interaction variance of a trait is the product of the within-locus additive genetic variances and is small relative to the additive genetic variance of the trait, as can be seen from V_A/V_{AA} and from order-of-magnitude arguments. The same would hold for the individual terms of the additive by additive interaction covariance versus the terms of the additive genetic covariance and for the other interaction components that can be compared to a main-effect variance component.

In the components of the phenotypic covariance between the traits F and S, all interaction components are necessarily negative, because the trade-off in allocation combines $+\gamma$ with $-\gamma$, or $+e$ with $-e$, in these covariance components (table 2). The additive genetic covariance, the dominance covariance, and the environmental covariance might be positive or negative (table 2), because the additive genetic, dominance, and environmental variances in acquisition contribute much to these covariance components. It is possible to find many combinations in sign: a positive additive genetic covariance together with a negative environmental covariance, or a positive additive genetic covariance and a phenotypic covariance that is negative owing to the interaction covariances. The signs

TABLE 2

TWO-LOCUS Y MODEL: COMPONENTS WITHIN THE PHENOTYPIC (CO)VARIANCE

(Co)Variance	In Trait F	In Trait S	Between Traits F and S
Additive genetic	$2pq\rho^2\overline{C}^2 + 2uv\gamma^2\overline{R}^2$	$2pq\rho^2(1-\overline{C})^2 + 2uv\gamma^2\overline{R}^2$	$2pq\rho^2\overline{C}(1-\overline{C}) - 2uv\gamma^2\overline{R}^2$
Dominance	$(2pqd)^2\overline{C}^2 + (2uve)^2\overline{R}^2$	$(2pqd)^2(1-\overline{C})^2 + (2uve)^2\overline{R}^2$	$(2pqd)^2(1-\overline{C})\overline{C} - (2uve)^2\overline{R}^2$
Environmental	$\sigma_R^2\overline{C}^2 + \sigma_C^2\overline{R}^2$	$\sigma_R^2(1-\overline{C})^2 + \sigma_C^2\overline{R}^2$	$\sigma_R^2\overline{C}(1-\overline{C}) - \sigma_C^2\overline{R}^2$
Interactions:			
Additive by additive	$2pq\rho^2 \cdot 2uv\gamma^2$	$2pq\rho^2 \cdot 2uv\gamma^2$	$-2pq\rho^2 \cdot 2uv\gamma^2$
Additive by dominant	$2pq\rho^2 \cdot (2uve)^2$	$2pq\rho^2 \cdot (2uve)^2$	$-2pq\rho^2 \cdot (2uve)^2$
Dominant by additive	$(2pqd)^2 \cdot 2uv\gamma^2$	$(2pqd)^2 \cdot 2uv\gamma^2$	$-(2pqd)^2 \cdot 2uv\gamma^2$
Dominant by dominant	$(2pqd)^2 \cdot (2uve)^2$	$(2pqd)^2 \cdot (2uve)^2$	$-(2pqd)^2 \cdot (2uve)^2$
Additive by environmental	$2pq\rho^2\sigma_C^2 + 2uv\gamma^2\sigma_R^2$	$2pq\rho^2\sigma_C^2 + 2uv\gamma^2\sigma_R^2$	$-2pq\rho^2\sigma_C^2 - 2uv\gamma^2\sigma_R^2$
Dominant by environmental	$(2pqd)^2\sigma_C^2 + (2pqe)^2\sigma_R^2$	$(2pqd)^2\sigma_C^2 + (2pqe)^2\sigma_R^2$	$-(2pqd)^2\sigma_C^2 - (2uve)^2\sigma_R^2$
Environmental by environmental	$\sigma_C^2\sigma_R^2$	$\sigma_C^2\sigma_R^2$	$-\sigma_C^2\sigma_R^2$

TABLE 3

TWO-LOCUS Y MODEL: COVARIANCES BETWEEN RELATIVES

Case	Covariance
Parent-offspring covariance	$\frac{1}{2}\,COV_A + \frac{1}{4}\,COV_{AA}$
Half-sib covariance	$\frac{1}{4}\,COV_A + COV_{AA}[\frac{1}{16} + \frac{1}{4}(\frac{1}{2} - \xi)^2]$

of the additive genetic covariance and the phenotypic covariance are virtually independent in this Y model containing both genetic and environmental sources of variation in acquisition and allocation.

In table 3, some covariances and cross-covariances between relatives are given for additive gene effects within a locus. In the parent-offspring covariance the coefficient of relationship appears, as set out in Falconer (1981, pp. 141–142). In the covariance among half-sibs the recombination probability appears even in linkage equilibrium (Cockerham 1956; Falconer 1981, p. 143). Multiplying the parent-offspring covariance by two or the covariance among half-sibs by four does not lead to an estimate of the additive genetic variance. For the case of additive gene action with linkage disequilibrium, the population variance, the covariance between parent and offspring, and the covariance among half sibs are given in Appendix B. The cross-covariances F/S and S/F between parents and offspring are no longer identical in this case.

SELECTION

Epistasis at the genetic level contributes strongly to the additive genetic variance: multiplicative gene action mimics the additive model. In classical quantitative genetics, the prediction of the selection response $\Delta\bar{z}$ for selection pressure on a trait z is the product of the heritability, $h^2 = V_A/V_P$, and the selection differential, s: $\Delta\bar{z} = h^2 s$ (Falconer 1981). For simultaneous selection pressure on a number of traits, the prediction for the vector of selection responses, $\mathbf{\Delta\bar{z}}$, from the genetic variance-covariance matrix, $\mathbf{G}$, the phenotypic variance-covariance matrix, $\mathbf{P}$, and the vector of selection differentials, $\mathbf{s}$, is as $\mathbf{\Delta\bar{z}} = \mathbf{GP^{-1}s}$ (Lande 1979); an alternative expression, $\mathbf{\Delta\bar{z}} = (1/\bar{w})\mathbf{G\nabla}\bar{w}$, involves the vector $\mathbf{\nabla}\bar{w}$ of the selection gradients and the partial derivatives, $\partial\bar{w}/\partial\bar{z}_i$, of mean fitness, $\bar{w}$, toward the trait means, $\bar{z}_i$. These predictions are exact for an additive model in two cases: the first case involves multivariate normal distributed traits and any fitness function, and the second case involves distributions of traits derived from multilocus genetics and fitness that is a linear function of the phenotype.

The Y model introduces a specific type of multiplicative gene action. What does that mean for selection? A major question is whether the predictions of the selection response of one trait by $h^2 s$ and the prediction of the vector of selection responses, $\mathbf{\Delta\bar{z}}$, by $\mathbf{GP^{-1}s} = (1/\bar{w})\mathbf{G\nabla}\bar{w}$ are valid, exactly or approximately, for multiplicative gene action in general or for the special case of the Y model.

Selection in a two-locus model for a quantitative trait can be dealt with by straightforwardly writing down the equations for two-locus selection on the one

hand and writing down the differences in the phenotypic means of the two traits between two generations on the other hand. This is done in Appendix C for a general multiplicative two-locus model and a fitness function that is linear in F and S and in the product FS. The conclusion in Appendix C is that selection pressure on one trait can be described by an expression analogous to $\Delta\bar{z} = h^2 s$ for general multiplicative gene action if the population is in linkage equilibrium and if the fitness function is linear in the trait considered; the predicted response to selection would be near to, but not be exactly equal to, twice the parent-offspring regression times the selection differential. Simultaneous selection pressure on two traits cannot be described by an expression analogous to $\mathbf{\Delta\bar{z}} = (1/\bar{w})\mathbf{G\nabla}\bar{w}$ for a general model of multiplicative gene action, even though most of the variation from multiplicative gene action converts to additive genetic variance (App.C); only in the Y model is a description of simultaneous selection pressure on the two traits F and S possible by an analogue of the classical $\mathbf{\Delta\bar{z}} = (1/\bar{w})\mathbf{G\nabla}\bar{w}$, if the population is in linkage equilibrium and fitness is linear in both traits.

To show this, let us consider simultaneous directional selection pressure on the traits F and S from the Y model, according to a fitness function for genotype $R_iR_jC_kC_l$ that is linear in the genotypic values for both traits:

$$w_{ijkl} = k_0 + k_1F_{ijkl} + k_2S_{ijkl}. \tag{4a}$$

The marginal fitnesses for locus R are

$$\bar{w}_{ij} = k_0 + k_1R_{ij}\bar{C} + k_2R_{ij}(1 - \bar{C}). \tag{4b}$$

The marginal fitnesses for locus C are

$$\bar{w}_{kl} = k_0 + k_1\bar{R}C_{kl} + k_2\bar{R}(1 - C_{kl}). \tag{4c}$$

The mean fitness is

$$\bar{\bar{w}} = k_0 + k_1\bar{R}\bar{C} + k_2\bar{R}(1 - \bar{C}), \tag{4d}$$

which indicates that k_1 is the selection gradient $\partial\bar{\bar{w}}/\partial\bar{F}$ and k_2 is the selection gradient $\partial\bar{\bar{w}}/\partial\bar{S}$.

Substituting the marginal fitnesses (eqq. [4b], [4c]) into the classical per locus selection formulas (see, e.g., Falconer 1981) yields for the case of linkage equilibrium

$$\Delta p = (1/\bar{\bar{w}})pq\rho[k_1\bar{C} - k_2(1 - \bar{C})] \tag{5a}$$

and

$$\Delta u = (1/\bar{\bar{w}})uv\gamma\bar{R}[k_1 - k_2]. \tag{5b}$$

Since in the Y model the differences between the mean values of traits F and S in two successive generations are, in linkage equilibrium,

$$\Delta\bar{F} = 2\rho\bar{C}\cdot\Delta p + 2\gamma\bar{R}\cdot\Delta u + 2\rho\cdot\Delta p\cdot 2\gamma\cdot\Delta u \tag{6a}$$

and

$$\Delta\bar{S} = 2\rho(1 - \bar{C}) \cdot \Delta p - 2\gamma\bar{R} \cdot \Delta u - 2\gamma \cdot \Delta u \cdot 2\rho \cdot \Delta p \qquad (6b)$$

(the third term is due to the multiplication of per locus genotypic values in the trait genotypic value), substitution of the changes in gene frequencies (eqq. [5a], [5b]) yields the expression for the simultaneous selection response for both traits, as

$$\begin{bmatrix} \Delta\bar{F} \\ \Delta\bar{S} \end{bmatrix} = (1/\bar{\bar{w}})\mathbf{G}' \begin{bmatrix} k_1 \\ k_2 \end{bmatrix}. \qquad (7)$$

This has the same form as $\Delta\bar{\mathbf{z}} = (1/\bar{w})\mathbf{G}\nabla\bar{w}$ (Lande 1979), although the matrix $\mathbf{G}'$ is not the additive genetic variance-covariance matrix, but a genetic variance-covariance matrix involving the additive by additive interaction too. If we define $\bar{W}$ as

$$\bar{W} \equiv (k_1\bar{F} + k_2\bar{S})/\bar{\bar{w}} = (k_1\bar{F} + k_2\bar{S})/(k_0 + k_1\bar{F} + k_2\bar{S}), \qquad (8)$$

a genetic variance-covariance matrix of the following form appears:

$$\mathbf{G}' = \begin{bmatrix} V_A(F) + V_{AA}(F) \cdot \bar{W} & COV_A(F,S) + COV_{AA}(F,S) \cdot \bar{W} \\ COV_A(F,S) + COV_{AA}(F,S) \cdot \bar{W} & V_A(S) + V_{AA}(S) \cdot \bar{W} \end{bmatrix}. \qquad (9)$$

How much influence does the additive by additive interaction variance exert on the selection response? We have to remember that V_{AA} is small relative to V_A, while COV_{AA} might be small relative to COV_A. We also have to evaluate $\bar{W} \equiv (k_1F + k_2S)/\bar{\bar{w}}$. For very weak selection, $k_0 \gg k_1, k_2$, and the factor $\bar{W}$ will approach zero; the matrix $\mathbf{G}'$ becomes the additive genetic variance-covariance matrix itself. For very strong selection, k_1 or k_2 will be large compared to k_0, and the factor $\bar{W}$ will approach 1; the influence of the interaction variance on selection will be maximal. But because

$$(CO)V_A < (CO)V_A + (CO)V_{AA} \cdot \bar{W} < (CO)V_A + (CO)V_{AA} \qquad (10)$$

while twice the parent-offspring covariance estimates $(CO)V_A + \frac{1}{2}(CO)V_{AA}$ (table 3), the usual estimates of additive genetic variance and covariance from a parent-offspring regression might perform quite satisfactorily in practice (while using four times the half-sib covariance would not; see table 3).

The result of selection is always fixation: at the highest or lowest genotypic value for the acquisition locus $\boldsymbol{R}$, depending on the value of $k_1\bar{C} + k_2(1 - \bar{C})$, and at the highest or lowest genotypic value of the allocation locus $\boldsymbol{C}$, depending on the sign of $k_1 - k_2$ (eqq. [5a], [5b]).

The selection expression (eq. [7]) is applicable to any acquisition-allocation schedule, independently of the number of loci at the acquisition level or the number of loci at the allocation level (fig. 2).

EVOLUTIONARILY STABLE STRATEGY (ESS) AND POLYMORPHISM IN ALLOCATION

In the preceding section, fitness was a linear function of both traits, and the result was a description of directional selection. Selectively maintained polymor-

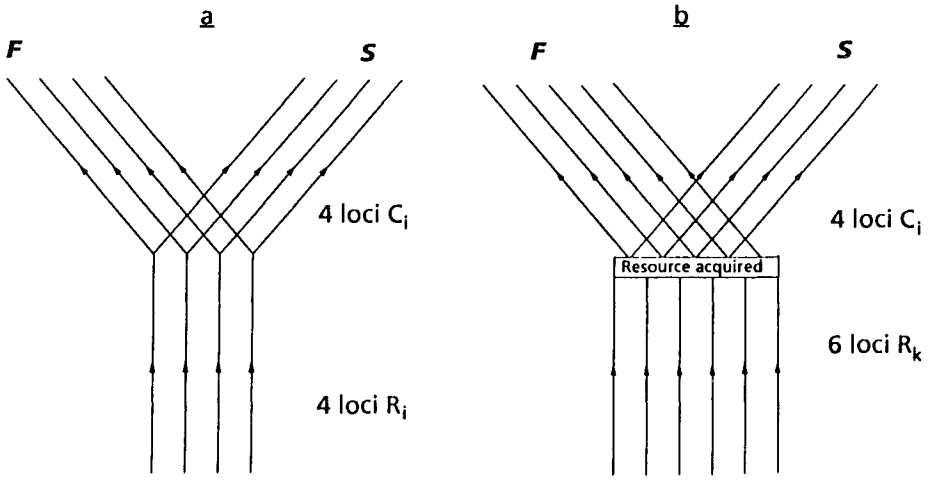

FIG. 2.—Polygenic Y models. *a*, Each acquisition locus is matched to an allocation locus; *b*, different number of acquisition loci.

phism is possible in the Y model if the fitness function includes the product of the two traits, FS. Selection pressure on the product implies that an intermediate fraction of allocation to F and S is selected for. Let w_{ijkl} be defined by

$$w_{ijkl} = k_0 + k_1 F_{ijkl} + k_2 S_{ijkl} + k_3 F_{ijkl} S_{ijkl}. \tag{11}$$

Selection formulas are found in Appendix C; no matrix formulation is possible. Polymorphism is unlikely for acquisition as it requires that $R/\rho < \frac{1}{2}$, which seems a biologically unlikely condition for an amount of resource and its variation. For positive selection gradients, k, it is more likely that locus R will be fixed at the highest genotypic value. A polymorphism in allocation can be maintained more easily. Locus C might be polymorphic, at an equilibrium frequency, $\hat{u}$, such that

$$\hat{u} = \tfrac{1}{2} + \overline{R}(k_1 - k_2)/[2\gamma(\overline{R}^2 + \sigma_R^2)k_3] + [(1 - C) - C]/2\gamma. \tag{12}$$

The range of values for which polymorphism is possible is fairly restricted; in figure 3, the shaded area gives the combinations of C and γ for which polymorphism might exist for the case $k_1 = k_2$. The conditions for polymorphism to be maintained correspond to those of Rose (1982) if $k_1 = k_2$.

The ESS value for C is found at the value of C that maximizes w in the absence of genetic variation; it is expected to evolve if there is a continuous supply of mutants with a small effect on allocation. From $\partial w/\partial C = 0$ it follows that the ESS value for C is

$$C_{\text{ESS}} = (k_3 R + k_1 - k_2)/(2k_3 R) = \tfrac{1}{2} + (k_1 - k_2)/(2k_3 R). \tag{13}$$

Neither the presence of a selectively maintained polymorphism at locus C nor the ESS value of the allocation fraction C constrains the covariance between the two traits F and S to be negative. In the case of a polymorphism in the allocation fraction that is maintained by selection pressure on the value of the product FS,

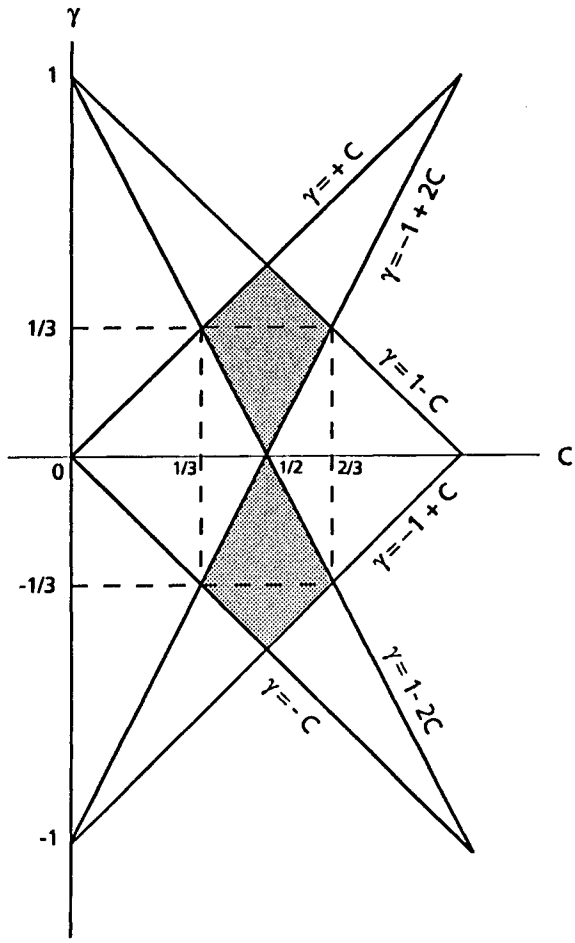

FIG. 3.—Area (*shaded*) of combinations of values of common allocation fraction, C, and average effect of a gene substitution, γ, that allow polymorphism at locus $\boldsymbol{C}$, if $k_1 = k_2$.

while locus $\boldsymbol{R}$ is fixed, the phenotypic covariance between the traits $\boldsymbol{F}$ and $\boldsymbol{S}$ becomes $\mathrm{COV}(F,S) = (1 - \overline{C}) \cdot \overline{C} \cdot \sigma_R^2 - [\overline{R}^2 + \sigma_R^2][2uv\gamma^2 + \sigma_C^2]$, and, while it seems likely that this is negative, it does not seem to be necessary. Antagonistic pleiotropy need not lead to a negative phenotypic covariance between two traits (cf. Charlesworth 1990). The additive genetic covariance (table 2) is, however, necessarily negative if there is no genetic variation at locus $\boldsymbol{R}$, but only the polymorphism at locus $\boldsymbol{C}$. At the ESS allocation fraction, genetic variation is absent at both loci, but the variation in acquisition and allocation due to environmental noise is still present. The covariance between the traits $\boldsymbol{F}$ and $\boldsymbol{S}$ becomes $\mathrm{COV}(F,S) = (1 - C) \cdot C \cdot \sigma_R^2 - (R^2 + \sigma_R^2)\sigma_C^2$, and this might be either positive or negative (van Noordwijk and de Jong 1986).

SELECTION AND LIFE HISTORIES

The two traits ***F*** and ***S*** in this genetic acquisition-allocation model might easily stand for life-history traits; life-history traits are very widely considered to result from physiological trade-offs (Sibly and Calow 1986). What is special for life-history traits is that they are directly involved in the determination of fitness. The implication is that acquisition of a resource and allocation of it to two competing life-history traits have a direct influence on fitness.

Genotypic fitness can be modeled in two ways: in a formal way in order to investigate the mathematical consequences of specific shapes of genotypic fitness, as we have been doing in expressions (4a) and (11), and in fitness components in order to investigate the influence of the life history on fitness and to link genotypic fitness to demography. Life-history representations for genotypic fitness can be found (see, e.g., de Jong 1990); if weak selection at stable age distribution and a constant growth rate of the population are assumed, genotypic fitness is numerically equal to

$$w_{ij} = \sum_{x=1}^{x=\infty} \lambda^{-x+1} l_{x,ij} b_{x,ij}, \tag{14}$$

where λ is the population growth rate at a stable age distribution, l_x is survival from birth to age x, and b_x is reproduction at age x. Survival, l_x, is found by multiplying the probabilities of survival, p_{k-1}, for survival from age $k-1$ to age k, over all age intervals up to age x:

$$l_{x,ij} = \prod_{k=1}^{k=x-1} p_{k,ij}. \tag{15}$$

Ages are assumed to be genetically independent, no locus affecting more than one age class. Genotypes will be supposed to differ in only one probability of survival and one age-specific fecundity, at age y. These are supposed to derive from an allocation of resources acquired within one period between reproductive events. This means that we will consider two forms for genotypic fitness, one in which the trade-off underlies p_{y-1} and b_y and one in which the trade-off underlies b_y and p_y.

Let us first consider the trade-off between p_{y-1} and b_y. An organism acquires energy between the $(y-1)$th time it reproduces, age $x = y-1$, and the next time it reproduces, age $x = y$. Part of this energy is spent immediately on metabolism and defense against parasites or herbivores; the remainder is saved or stored for the next future reproduction at age $x = y$. Energy is allocated to survival (p_{y-1}), and the remainder is used for reproduction (b_y). The probability p_{y-1} plays the role of the trait ***F***: it is the trait to which energy is actively allocated, the determining trait. Reproduction, b_y, plays the role of trait ***S***, the trait that gets what is left.

Both traits appear in demographic fitness in $l_y b_y \lambda^{-y+1}$; moreover, trait ***F*** ap-

pears in $\Sigma_{x=y+1}^{x=\infty} \lambda^{-x+1} l_x b_x$. Selection is on the product of the traits, $\boldsymbol{FS}$, at age y and involves trait $\boldsymbol{F}$ at all later ages. Trait $\boldsymbol{S}$ appears only at age y, in the product $\boldsymbol{FS}$. Therefore, if allocation is first to viability while only the remainder or surplus energy goes to reproduction, a formal fitness model like expression (11) is appropriate. The coefficients (k_0, k_1, k_2, k_3) in expression (11) stand partly for life-history components and partly for scaling factors that were not further considered. The determination of the coefficients is by age: at the trade-off age, before the trade-off, and after the trade-off. The coefficient k_0 represents the age classes before the trade-off, $k_0 = \Sigma_{x=1}^{x=y-1} \lambda^{-x+1} l_x b_x$. The coefficient k_1 of trait $\boldsymbol{F}$ represents the influence of the later age classes, as the viability p_{y-1} influences survival to all later ages: $k_1 = (1/p_{y-1}) \Sigma_{x=y+1}^{x=\infty} \lambda^{-x+1} l_x b_x$. Reproduction at age $x = y$ appears only in the product $\boldsymbol{FS}$ in genotypic fitness, and this precludes a separate selection gradient on $\boldsymbol{S}(b_y)$ from appearing; that is, $k_2 = 0$. The coefficient k_3, described by $k_3 = l_{y-1}\lambda^{-y+1}$, of the product $\boldsymbol{FS}$ (equal to $p_{y-1}b_y$) represents selection at age y.

The ESS allocation fraction to viability, p_{y-1}, becomes (see eq. [13])

$$C_{\text{ESS}} = (k_3 R + k_1)/(2k_3 R) = \tfrac{1}{2} + \tfrac{1}{2} \cdot (k_1/k_3) \cdot (1/R). \tag{16a}$$

The ESS allocation fraction C_{ESS} involves $k_1/k_3 = (\lambda^y/l_y) \Sigma_{x=y+1}^{x=\infty} \lambda^{-x} l_x b_x = (p_{y-1}/\lambda) \cdot V_{y+1}$ (where V_{y+1} stands for the reproductive value at age $y + 1$):

$$C_{\text{ESS}} = \tfrac{1}{2} + \tfrac{1}{2} \cdot (1/R) \cdot (p_{y-1}/\lambda) \cdot V_{y+1}. \tag{16b}$$

This implies that the allocation to viability at any age is at least half the energy acquired. Acquisition of resources, and fitness components after the age of trade-off and at the trade-off, plays different roles in determining the ESS allocation fraction. Fitness components before the trade-off do not influence C_{ESS}. A trade-off at age y is demographically independent of the previous ages, if it is genetically independent, as is supposed here.

If the species is iteroparous, the amount of resource actually acquired between two reproductive events has an influence on the evolutionarily stable life-history strategy for allocation. Since R is an amount of energy or some other resource, $R > 1$ seems reasonable. The ESS allocation fraction to viability increases from $\frac{1}{2}$ to $\frac{1}{2}(1 + k_1/k_3)$ if the amount acquired, R, decreases from infinity to one. In a poor environment, allocation of energy to viability will therefore be favored over allocation to reproduction. The ESS allocation to viability will counteract the direct influence of an environment that decreases viability and promotes survival at the expense of reproduction.

The ESS allocation fraction depends on the age considered, as at least k_1 depends on the age class. In a poor environment the potential age structure of an iteroparous species has a pronounced effect on the ESS allocation fraction, as a higher expectation of survival and reproduction at later ages increases the coefficient k_1. For potential high survival to high age the ESS allocation to survival at the age considered for the trade-off receives an additional boost. Survival feeds back on itself. Another implication is that the ESS allocation to viability at different ages will decrease with age; if we compare a trade-off between p_1 and b_2 with a trade-off between p_8 and b_9, for instance, the ESS allocation fraction to viability

will be higher for the earlier age. Reproduction might increase with age but never cost more than half the energy available.

In a rich environment or at a high population growth rate, λ, the ESS allocation fraction to viability will be lower, approaching half the energy acquired: reproduction is favored when there is enough to survive. The influence of the remaining ages (k_1) would be lower in a rich environment than in a poor environment, and the ESS allocation fraction will vary less between ages.

The second possibility is a trade-off between b_y and p_y. This case has been dealt with in models of "reproductive effort" (Schaffer 1979). Of an acquired energy supply, part is allocated to reproduction, and the remainder is used toward survival to the next breeding age. Now it is reproduction, b_y, that plays the role of the trait $\boldsymbol{F}$ to which the resource is actively allocated, while survival until the next breeding age, p_y, plays the role of the default trait $\boldsymbol{S}$. In the life-history expression for genotypic fitness, b_y and p_y appear in different terms.

This means that a formal fitness model like expression (4a) is appropriate if allocation is first to fecundity while only the remainder of the energy goes to viability. The formal coefficients stand for the other life-history components: k_1 for $\lambda^{-y+1} l_y$, k_2 for $(1/p_y) \sum_{x=y+1}^{x=\infty} \lambda^{-x+1} l_x b_x$, and k_0 for $l_{y-1} b_{y-1}$. We have already seen that the ESS allocation fraction, C_{ESS}, is either zero or one in this model. Either reproduce all out, or not at all. Therefore, the time sequence of energy acquisition and allocation to fitness components has large consequences for the life-history strategy.

DISCUSSION

The Y models we describe provide a connection between quantitative genetics and life-history theory, population genetics and physiology. A Y model as presented here is written in the biological properties of genes: the approach is by way of population genetics, but it is clear that the variances and covariances between traits are fully compatible with the quantitative genetic approach. The biological properties of the genes as assumed in the model are physiological, but the biological conclusions pertain to life-history theory. That is, we present Y models as a thinking substrate for connecting fields in a biological way. We claim that the model provides both new results and derivations of known results that are easier to interpret.

In an earlier article we presented a simple nongenetic Y model of acquisition and allocation of resources to explain the occurrence of positive phenotypic correlations where negative phenotypic correlations were expected because of a trade-off (van Noordwijk and de Jong 1986). A developmental version of a Y model was given by Riska (1986). Compatible but mathematically more complicated and less mechanistic models of constraints due to trade-offs in quantitative genetics and their consequences on genetic covariances are given by Pease and Bull (1988) and Charlesworth (1990).

Epistasis and Selection

The different uses of "epistasis" become visible. Epistasis at the gene level is modeled as the multiplication of the per locus genotypic effects. In the variance

components of quantitative genetics, the existence of the interaction variances is due to this multiplication, but the numerically largest effect of epistasis at the gene level is in the additive genetic variance.

Locus R influences the acquisition of the resource and would be both a "biochemical gene" and a "quantitative gene." Locus C allocates and converts a resource to trait F: it is both a biochemical gene and a quantitative gene with regard to trait F. Trait S gets the amount of resource, $1 - C$, that is left after the allocation to trait F; therefore, locus C is the quantitative gene for trait S, but it might be quite another locus that actually converts the resource to trait S. This other locus might even show biochemical genetic variation that is not expressed as quantitative variation. Biochemical and quantitative genetic variation in a trait need not be related at all.

A prediction of the selection responses in the two traits deriving from the trade-off can be found for directional selection. The prediction involves a matrix $\mathbf{G}'$ containing the additive by additive interaction variances and covariances as well as the additive genetic (co)variances. The prediction is analogous to the classical prediction of the vector of selection responses $\Delta\bar{\mathbf{z}}$ from the product of the genetic variance-covariance matrix, $\mathbf{G}$, and the vector of logarithmic selection gradients, $\nabla \ln \bar{w}$. A prediction of the selection responses based on the parent-offspring covariances will be near the exact selection response; a prediction based on the additive genetic (co)variances themselves will be very near the exact selection response for weak selection. This shows that the actual developmental composition of the traits has little influence on phenotypic changes under weak selection.

There is no basis for the convergence of the additive genetic correlation and the phenotypic correlation in an additive model. In the Y model, such convergence is at least possible. If all interaction components in the phenotypic variance (table 2, "Interactions") are very small, and if the environmental and genetic variances at a level are of the same order of magnitude, the genetic correlation and the phenotypic correlation might approximate each other in the Y model. Cheverud (1988) showed that most existing data sets provide evidence that additive genetic and phenotypic correlations rather than additive genetic and phenotypic covariances are quite similar.

Life-History Strategies

In life-history theory, many trade-off models exist, but they mostly involve supposing a direct trade-off between traits without considering underlying processes. An exception is the model of Sibly and Calow (1984); they related a difference for life-history strategies to the time sequence of paying the cost of reproduction. Reproduction paid for from energy collected before reproduction was termed "direct costing," corresponding to allocation first to viability, with the remainder to fecundity. Reproduction paid later was termed "absorption costing," corresponding to allocation to fecundity first, with the remainder to subsequent viability. Some of Sibly and Calow's conclusions correspond to the life-history conclusions here, such as that reproduction is lower with direct costing. But the main difference is that Sibly and Calow write the fitness function for

direct costing differently from that for absorption costing; direct costing skips the first reproduction compared with absorption costing.

In the model by Schaffer (1974*a*, 1974*b*) on iteroparity and semelparity, survival is actually the survival following in time upon reproduction (Schaffer 1979). In the simple Y model, iteroparity is not an evolutionarily stable strategy if survival is the "remainder" trait: there is always either total investment in survival or total investment in reproduction. The difference is due to the nonlinear transformation between reproductive effort and survival or fecundity used by Schaffer (1974*a*, 1974*b*); in the Y model only linear scaling is used. As in the model of Schaffer (1974*a*, 1974*b*; 1979), optimization is per age class—this because it is supposed that the acquisition and allocation of resources are genetically independent between age classes, a different set of genes being responsible for acquisition and allocation at each age. If the same genes were responsible for acquisition and allocation at each age, one would have to do a simultaneous optimization over all ages (Caswell 1980). The difference between the models of Caswell (1980) and Schaffer (1974*a*, 1974*b*, 1979) can be seen as a difference of opinion about the genetic independence of allocation processes between age classes. Genetic independence between age classes leads to optimization per age class, as in Schaffer's model, and genetic identity leads to the much more restrictive simultaneous optimization over all age classes, as in Caswell's model. Yodzis (1981) pointed out the difference in the optimization criterion used but did not suggest that implicit assumptions about genetic relationships between traits were in fact playing a role.

A trade-off between reproduction and subsequent survival recalls models of life-history predictions based on a trade-off between current reproduction and residual reproductive value (Pianka and Parker 1975; Pianka 1976). In Pianka (1976) and Schaffer (1979), maximizing fitness means maximizing reproductive value. However, here we have two ways to structure the physiological trade-off, and only one, in which the trade-off is between reproduction and subsequent survival, corresponds to the trade-off between life-history components as used by Pianka (1976) and Schaffer (1974*a*, 1974*b*; 1979).

The other physiological trade-off, between survival and subsequent reproduction, leads to another relation between fitness and reproductive value, as recognized by Schaffer (1979) and Caswell (1980). This trade-off translates into a fitness function that does not involve the sum of the traits, but one of the traits and their product. Maximizing fitness involves both p_{y-1} itself and the product $p_{y-1}b_y$, that is, the residual reproductive value at age $y - 1$, $p_{y-1}\lambda^{-1}V_{y+1}$, not the reproductive value, V_y, itself. The strict relation between maximizing fitness and maximizing reproductive value depends on a particular life-history assumption. The same assumption that makes maximizing fitness equivalent to maximizing reproductive value in a model of life-history evolution causes the classical model of simultaneous selection on two quantitative traits, $\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s}$, to be (approximately) valid. The models of Lande (1982) and Schaffer (1979) belong together. Neither gives a general model of life-history evolution, because the evolution of fitness components that appear as a product in the demographic expression for fitness cannot be handled by either model.

APPENDIX A

List of Symbols

b_x	Reproduction at age x
$\boldsymbol{C}$	Locus determining allocation
C	Basic fraction allocated by all genotypes to trait $\boldsymbol{F}$
$\overline{C}$	Mean genotypic value at locus $\boldsymbol{C}$ for allocation to trait $\boldsymbol{F}$
C_{ESS}	Evolutionarily stable strategy value for C
C_{kl}	Genotypic value for allocation to trait $\boldsymbol{F}$, genotype $\boldsymbol{C}_k\boldsymbol{C}_l$
c_{kl}	$C_{kl} - C$
D	Linkage disequilibrium, $x_{11}x_{22} - x_{12}x_{21}$
d	Dominance deviation at locus $\boldsymbol{R}$ on acquisition
$\Delta\bar{z}$	Selection response in trait z
$\mathbf{\Delta\bar{z}}$	Vector of selection responses for traits z_i
e	Dominance deviation at locus $\boldsymbol{C}$ for allocation
ϵ_C	Individual value for environmental error at the allocation level, $\overline{\epsilon_C} = 0$
ϵ_R	Individual value for environmental error at the acquisition level, $\overline{\epsilon_R} = 0$
$\boldsymbol{F}$	Name of trait receiving allocation fraction C
F	Value of trait $\boldsymbol{F}$
$\overline{F}$	Mean value of trait $\boldsymbol{F}$
$\mathbf{G}$	Additive genetic variance-covariance matrix
$\mathbf{G}'$	Variance-covariance matrix involving additive genetic and additive by additive interaction variance components
$\mathbf{GP^{-1}s}$	Prediction of the vector of selection responses $\mathbf{\Delta\bar{z}}$
γ	Average effect of a gene substitution at locus $\boldsymbol{C}$ for allocation
$\gamma\overline{R}$	Average effect of a gene substitution at locus $\boldsymbol{C}$ for trait $\boldsymbol{F}$
$-\gamma\overline{R}$	Average effect of a gene substitution at locus $\boldsymbol{C}$ for trait $\boldsymbol{S}$
h^2	Heritability of a trait, V_A/V_P
$h^2 s$	Prediction of the selection response
k_0	Basic fitness value
k_1	Selection gradient for trait $\boldsymbol{F}$
k_2	Selection gradient for trait $\boldsymbol{S}$
k_3	Selection gradient on the product of the trait values, FS
ξ	Recombination fraction between loci $\boldsymbol{R}$ and $\boldsymbol{C}$
l_x	Survival probability from birth to age x
λ	Population growth rate at stable age distribution
$1 - \overline{C}$	Mean genotypic value at locus $\boldsymbol{C}$ for allocation to trait $\boldsymbol{S}$
$\mathbf{P}$	Phenotypic variance-covariance matrix
p, q	Gene frequencies at locus $\boldsymbol{R}$, $q = 1 - p$
p_{x-1}	Survival probability from age $x - 1$ to age x
$\boldsymbol{R}$	Locus determining acquisition
R	Basic amount of resource acquired by all genotypes
$\overline{R}$	Mean genotypic value at locus $\boldsymbol{R}$
R_{ij}	Genotypic value for acquisition, genotype $\boldsymbol{R}_i\boldsymbol{R}_j$
r_{ij}	$R_{ij} - R$
ρ	Average effect of a gene substitution at locus $\boldsymbol{R}$ on acquisition
$\rho\overline{C}$	Average effect of a gene substitution at locus $\boldsymbol{R}$ for both traits $\boldsymbol{F}$ and $\boldsymbol{S}$
$\boldsymbol{S}$	Name of trait receiving allocation fraction $1 - C$
S	Value of trait $\boldsymbol{S}$
$\overline{S}$	Mean value of trait $\boldsymbol{S}$
s	Selection differential, $\overline{ws} = \mathrm{cov}(z, w)$
$\mathbf{s}$	Vector of selection differentials for traits z_i

σ_C^2	Variance of ϵ_C
σ_R^2	Variance of ϵ_R
u, v	Gene frequencies at locus $\boldsymbol{C}$, $v = 1 - u$
$V_A(F)$	Additive genetic variance of trait $\boldsymbol{F}$
V_y	Reproductive value at age y, $\sum_{x=y}^{x=\infty} \lambda^{-x} l_x b_x$
var(F)	Phenotypic variance of trait $\boldsymbol{F}$
$\overline{W}$	$(k_1\overline{F} + k_2\overline{S})/(k_0 + k_1\overline{F} + k_2\overline{S})$
w	Fitness
$\overline{w}$	Mean fitness
$\nabla\overline{w}$	Vector of selection gradient $\partial\overline{w}/\partial\overline{z}_i$
x, y	Age
x_{ik}	Frequency of gamete $\boldsymbol{R}_i\boldsymbol{C}_k$
z	General designation of a trait
z_i	Mean value of trait i

APPENDIX B

Influence of Linkage Disequilibrium on the Variances and Covariances of $\boldsymbol{F}$ and $\boldsymbol{S}$

When linkage disequilibrium exists, the genetic variance has additional components due to linkage disequilibrium. We will mention these only for two additive loci, not dominance. Linkage disequilibrium can be given as $D = x_{11}x_{22} - x_{12}x_{21}$, where x_{ik} is the frequency of the gamete with $\boldsymbol{R}_i\boldsymbol{C}_k$. The expression (CO)$V_A(I,J)$, and so on, will be as in table 1. In the case of linkage disequilibrium,

$$\mathrm{COV}_G(I,J) = \mathrm{COV}_A(I,J) + \mathrm{COV}_{AA}(I,J) + 2D\rho\gamma R(C_I + C_J) \pm 2D\rho\gamma(\overline{R} - R)(\overline{C} - C)$$

($I = F,S$; $J = F,S$). In $\mathrm{COV}_G(F,S)$ the sign of the last term is positive; in $V_G(F)$ and $V_G(S)$ the sign of the last term is negative. To obtain $V_G(F)$, $C_I = C_J = C$; to obtain $V_G(S)$, $C_I = C_J = -(1 - C)$; to obtain $\mathrm{COV}_G(F,S)$, $C_I = -C$, $C_J = (1 - C)$.

In the parent-offspring covariances, P stands for parental value, and O for the offspring mean. Linkage disequilibrium causes the recombination frequency to appear.

$$\mathrm{COV}(P{:}I;O{:}J) = \tfrac{1}{2}\mathrm{COV}_A(I,J) + \tfrac{1}{4}\mathrm{COV}_{AA}(I,J) + D\rho\gamma[RC_I(1 - \xi) + C_I\overline{R} + R\overline{C}_J - \overline{R}\overline{C}_I(1 - \xi)] \pm 2D^2\rho^2\gamma^2(\tfrac{1}{2} - \xi)$$

($I = F,S$; $J = F,S$). In $\mathrm{COV}(P{:}F;O{:}S)$ and $\mathrm{COV}(P{:}S;O{:}F)$ the sign of the last term is positive; in $\mathrm{COV}(P{:}F;O{:}F)$ and $\mathrm{COV}(P{:}S;O{:}S)$ the sign of the last term is negative. To obtain $\mathrm{COV}(P{:}F;O{:}F)$, $C_I = C_J = C$; to obtain $\mathrm{COV}(P{:}S;O{:}S)$, $C_I = C_J = -(1 - C)$; to obtain $\mathrm{COV}(P{:}F;O{:}S)$, $C_I = -C$ and $C_J = (1 - C)$; to obtain $\mathrm{COV}(P{:}S;O{:}F)$, $C_I = 1 - C$ and $C_J = -C$. The two parent-offspring cross-covariances are equal only when there is linkage equilibrium.

The covariances between half-sibs can be written in similar forms:

$$\begin{aligned}\mathrm{COV}(H{:}I,J) = {} & \tfrac{1}{4}\mathrm{COV}_A(I,J) + \mathrm{COV}_{AA}(I,J)[\tfrac{1}{16} + \tfrac{1}{4}(\tfrac{1}{2} - \xi)^2] \\ & + \tfrac{1}{4}D\rho\gamma(1 - \xi)\cdot[+RC_I(1 - \xi) + \overline{R}C_I(1 + \xi) + R\overline{C}_I(1 + \xi) - \overline{R}\overline{C}_I(1 + \xi)] \\ & + \tfrac{1}{4}D\rho\gamma(1 - \xi)\cdot[+RC_J(1 - \xi) + \overline{R}C_J(1 + \xi) + R\overline{C}_J(1 + \xi) - \overline{R}\overline{C}_J(1 + \xi)] \\ & \pm D^2\rho^2\gamma^2(\tfrac{1}{2} - \xi)\end{aligned}$$

($I = F,S$; $J = F,S$). To obtain $\mathrm{COV}(H{:}F)$, $C_I = C_J = C$; to obtain $\mathrm{COV}(H{:}S)$, $C_I = C_J = -(1 - C)$; to obtain $\mathrm{COV}(H{:}F,S)$, $C_I = -C$ and $C_J = (1 - C)$. The covariances between half-sibs are not simply related to the population variance or to the covariances between parent and offspring. Four times the covariance between half-sibs cannot be used in the prediction of selection.

APPENDIX C

Selection Pressure on Multiplicative Traits

The problem is to see how far the quantitative genetic selection formulas for two traits are valid for traits that are formed additively within but multiplicatively between loci. Linkage disequilibrium is absent.

Consider two traits, F and S, that are multiplicatively put together from gene effects at two loci. The effects within the loci are assumed to be additive. Genotype A_iA_j at locus A contributes $A + a_i + a_j$ to trait F and $C + c_i + c_j$ to trait S. Genotype B_kB_l at locus B contributes $B + b_k + b_l$ to trait F and $D + d_k + d_l$ to trait S. The gene frequency of allele A_1 equals p, and of allele A_2, q, where $q = 1 - p$. The gene frequency of allele B_1 equals u, and of allele B_2, v, where $v = 1 - u$. Genotype $A_iA_jB_kB_l$ leads to a genotypic value for trait F of $(A + a_i + a_j)(B + b_k + b_l)$ and of $(C + c_i + c_j)(D + d_k + d_l)$ for trait S. The mean genotypic value for trait F is $F = (\overline{AB}) = \overline{A}\overline{B}$ because of the independence of the loci, and for trait S it is $\overline{S} = \overline{C}\overline{D}$. The average effect of a gene substitution at locus A for trait F is $\alpha = \frac{1}{2}\,\partial\overline{A}/\partial p = a_1 - a_2$; the average effects β, γ, and δ are analogously defined (Kojima 1959).

The environment might contribute some noise. Let us suppose that there are four instances of random environmental effects: ϵ_A added to A, ϵ_B added to B, ϵ_C added to C, and ϵ_D added to D. The environmental effects have a mean of zero and variances of σ^2_A, σ^2_B, σ^2_C, and σ^2_D. Environmental effects of different levels are independent, but those at the same level have a covariance: that is, $\mathrm{cov}(\epsilon_A,\epsilon_C) \neq 0$ and $\mathrm{cov}(\epsilon_B,\epsilon_D) \neq 0$. Effects A and C, and B and D, are not independent. Therefore, $(\overline{AC}) = \overline{A}\cdot\overline{C} + 2pq\cdot\alpha\gamma + \mathrm{cov}(\epsilon_A,\epsilon_C)$ and $(\overline{BD}) = \overline{B}\cdot\overline{D} + 2uv\cdot\beta\delta + \mathrm{cov}(\epsilon_B,\epsilon_D)$.

The fitness function most related to selection gradients is in its general shape (see expression [11]) $w = k_0 + k_1F + k_2S + k_3FS = k_0 + k_1AB + k_2CD + k_3ABCD$. The changes in gene frequency are, according to standard procedure,

$$\Delta p = (pq/\overline{w})\{k_1\overline{B}\alpha + k_2\overline{D}\gamma + k_3(\overline{BD})[\alpha C + \gamma A + \alpha\gamma(p - q)]\}$$

and

$$\Delta u = (uv/\overline{w})\{k_1\overline{A}\beta + k_2\overline{C}\delta + k_3(\overline{AC})[\beta D + \delta B + \beta\delta(u - v)]\}.$$

The change in the mean value of trait F between any two generations 0 and 1 can be written as (with index indicating generation number) $\Delta\overline{F} = \overline{F}_1 - \overline{F}_0 = \overline{A}_1\overline{B}_1 - \overline{A}_0\overline{B}_0 = 2\alpha\overline{B}\cdot\Delta p + 2\beta\overline{A}\cdot\Delta u + 4\alpha\beta\cdot\Delta p\cdot\Delta u$ under the condition of linkage equilibrium. Substitution of Δp and Δu shows that this cannot be written as an expression in genetic variances and covariances, even when $k_3 = 0$. A simple prediction of $\Delta\overline{F}$ and $\Delta\overline{S}$ in an expression involving additive genetic variance and covariance, and additive by additive interaction variance and covariance, is not possible for linear selection pressure on two traits in a general model of multiplicative genetic effects. But when there is selection pressure on only one trait—for instance, F ($k_2 = 0$, $k_3 = 0$)—the change in mean phenotypic value for trait F becomes (see expression [7]) $\Delta\overline{F} = (1/\overline{w})\cdot k_1[\mathrm{V_A}(F) + \mathrm{V_{AA}}(F)\cdot\overline{W}]$. For one trait, a prediction of the selection response is possible for multiplicative gene action; the expression involves not the parent-offspring covariance, $\mathrm{V_A}(F) + \frac{1}{2}\,\mathrm{V_{AA}}(F)$, but $\mathrm{V_A}(F) + \mathrm{V_{AA}}(F)\cdot\overline{W}$ $(0 < \overline{W} < 1)$. This might be near enough numerically, as $\mathrm{V_{AA}}(F)$ might be smaller than $\mathrm{V_A}$ by an order of magnitude, but it shows that the parent-offspring regression line is no starting point for the prediction of the selection response in general.

In the Y model, special relations hold. Let locus A stand for locus R and locus B stand for locus C. Then $A = C \equiv R$, $B = 1 - D \equiv C$, $a_i = c_i \equiv r_i$, $b_k = -d_k \equiv c_k$, and $\overline{A} = \overline{C} \equiv \overline{R}$, $\overline{B} \equiv \overline{C}$, $\overline{D} \equiv 1 - \overline{C}$, $\alpha = \gamma \equiv \rho$, $\beta \equiv \gamma$, $\delta \equiv -\gamma$, $\mathrm{cov}(\epsilon_A,\epsilon_C) = \sigma^2_R$, and $\mathrm{cov}(\epsilon_B,\epsilon_D) = \sigma^2_C$. Substitution leads to a change in the mean value for trait F between two generations

of

$$\begin{aligned}\Delta\bar{F} = (1/\bar{w}) \cdot \{&k_1 V_A(F) + k_2 COV_A(F,S) \\ &+ 4pquv\rho^2\gamma^2(1/\bar{w})[k_1\bar{R}\bar{C} + k_2\bar{R}(1-\bar{C})]k_1 \\ &- 4pquv\rho^2\gamma^2(1/\bar{w})[k_1\bar{R}\bar{C} + k_2\bar{R}(1-\bar{C})]k_2\},\end{aligned}$$

and, when expression (8) is used, this leads to

$$\Delta\bar{F} = (1/\bar{w}) \cdot [k_1 V_A(F) + k_2 COV_A(F,S) + k_1 V_{AA}(F) \cdot \bar{W} + k_2 COV_{AA}(F,S) \cdot \bar{W}].$$

Similarly,

$$\Delta S = (1/\bar{w}) \cdot [k_1 COV_A(F,S) + k_2 V_A(S) + k_1 COV_{AA}(F,S) \cdot \bar{W} + k_2 V_{AA}(S) \cdot \bar{W}].$$

Therefore, simultaneous selection pressure on both traits leads to expressions (7) and (9). The result hinges on the fact that one of the two loci has the same effect on both traits, and the other locus an exactly opposite effect.

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Associate Editor: Mark Kirkpatrick