Consequences of Hierarchical Allocation for the Evolution of Life-History Traits

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ABSTRACT: Resource allocation within individuals may often be hierarchical, and this may have important effects on genetic correlations and on trait evolution. For example, organisms may divide energy between reproduction and somatic growth and then subdivide reproductive resources. Genetic variation in allocation to pathways early in such hierarchies (e.g., reproduction) can cause positive genetic correlations between traits that trade off (e.g., offspring size and number) because some individuals invest more resources in reproduction than others. We used quantitative-genetic models to explore the evolutionary implications of allocation hierarchies. Our results showed that when variation in allocation early in the hierarchy exceeds subsequent variation in allocation, genetic covariances and initial responses to selection do not reflect trade-offs occurring at later levels in the hierarchy. This general pattern was evident for many starting allocations and optima and for whether traits contributed multiplicatively or additively to fitness. Finally, artificial selection on a single trait revealed masked trade-offs when variation in early allocation was comparable to subsequent variation in allocation. This result confirms artificial selection as a powerful, but not foolproof, method of detecting trade-offs. Thus, allocation hierarchies can profoundly affect life-history evolution by causing traits to evolve in the opposite direction to that predicted by trade-offs.

Keywords: correlated response to selection, quantitative genetics, resource allocation, simulation study, trade-off.

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Trade-offs due to finite resources are thought to place a universal constraint on the evolution of life-history traits because genotypes that invest heavily in one trait or activity must reduce their investment in other traits (Roff 1992; Stearns 1992). At the population level, trade-offs are expected to cause negative genetic covariances and correlations between traits involved in trade-offs. In quantitative-genetic terms, correlations between multiple traits are described by **G**, the matrix of genetic variances and covariances among traits (Lande 1979; Falconer and Mackay 1996). Some trade-offs are reasonably well demonstrated. For example, reproductive costs in the form of either lower survival or reduced somatic growth and future reproduction have been reported in many animals and plants (e.g., Bell and Koufopanou 1986; Snow and Whigham 1989; Calvo 1993) and appear to form a general constraint on life-history evolution. Other finer-scale trade-offs may be less easily detected. For example, hermaphrodites use resources invested in reproduction to produce gametes of both sexes, introducing a potential trade-off between female and male allocation. Indeed, comparisons of sexes in dimorphic plant species support this trade-off (reviewed by Goldman and Willson 1986; Mazer et al. 1999). However, negative genetic correlations between female and male function have rarely been detected within hermaphroditic populations (Mazer et al. 1999), even though most dimorphic taxa have hermaphroditic ancestors. Thus, trade-offs that are expected to have an important influence on life-history traits are not always evident from **G**.

Several situations can cause positive correlations between the traits involved in life-history trade-offs. Charlesworth (1990) showed analytically that positive genetic correlations are possible among multiple traits subject to functional constraints. Phenotypic and genetic variation in resource acquisition can cause positive correlations between traits that are expected to compete for resources (Bell and Koufopanou 1986; van Noordwijk and de Jong 1986; Houle 1991). Houle (1991) emphasized the importance of considering the genetic architecture linking life-history traits, that is, the number and action of loci contributing to acquisition and allocation. Because many traits

affect an organism's ability to acquire resources, loci affecting acquisition are likely to outnumber those influencing allocation between any pair of traits, so that genetic variation for acquisition may exceed that for allocation (Charlesworth 1990; Houle 1991). De Laguerie et al. (1991) and de Jong (1993) extended the classic Y model of acquisition/allocation to recognize that many life-history traits probably result from a series of allocations made in a hierarchical manner. For example, plants may allocate resources between reproduction and vegetative functions and then subdivide reproductive resources between female and male function. Similarly, male animals may subdivide reproductive resources between mate attraction and gamete production. High variation in allocation to pathways early in the hierarchy (e.g., to reproductive vs. somatic tissues) may obscure trade-offs further along the hierarchy because some individuals invest more resources in reproduction than others (de Laguerie et al. 1991; de Jong 1993).

Thus, there are several reasons why **G** may not always reflect evolutionary constraints, and these reasons have received a good deal of attention in the context of the detection of trade-offs (Reznick 1985, 1992; Bell and Koufopanou 1986; de Laguerie et al. 1991; Houle 1991; de Jong 1993). They also raise questions about the evolutionary implications of the commonly observed positive or nonsignificant genetic correlations between traits involved in trade-offs. We were interested in how hierarchical allocation affected the evolution of traits involved in trade-offs. To use our earlier example, what are the evolutionary consequences of a trade-off between female and male function if genetic variation in allocation to reproduction causes a positive genetic correlation between female and male traits?

Here, we argue that considering allocation hierarchies has the potential to yield insight into the question posed above. First, as explained earlier, variation in allocation early in hierarchies may cause positive genetic covariances between life-history traits. Second, expected genetic variances and covariances can be predicted from allocation fractions and their variances. The effects of evolutionary changes in allocation on **G** are therefore also predictable. Finally, allocation hierarchies allow us to predict how different amounts of genetic variation in allocation at each level of a hierarchy will influence life-history evolution. This is because $R = G\beta$, where R is the vector of responses and β the vector of selection gradients (Lande 1979, 1982). The second of these perspectives has been explored by de Jong (1993), who considered how changes in allocation fractions affect the likelihood of negative genetic correlations. The evolutionary implications of variation in allocation hierarchies have apparently not been considered. Here, we use quantitative-genetic models and computer simulations to explore how allocation hierarchies affect the evolution of life-history traits involved in trade-offs.

We ask the following specific questions about traits involved in a two-level hierarchy. First, how does relative variation in allocation at each level of the hierarchy influence the direction and rate of evolution? Second, how does relative variation within the hierarchy affect the time until a trade-off becomes evident from responses to selection, that is, increases in one trait that are accompanied by decreases in another trait? We consider each of these questions under scenarios that model both natural and artificial selection.

Development of the Model

We assumed that finite resources were allocated to three measured traits, T_1, T_3, and T_4, which were all under positive directional selection. The structure of the model implies infinite, randomly mating populations with no linkage disequilibrium, no epistasis, and no interactions between genotype and environment. All calculations and simulations were performed using Maple V, release 5.1 (Waterloo Maple, Waterloo, Ontario).

Hierarchical Allocation and Genetic Variation

We considered a two-level allocation hierarchy (fig. 1). Of the R_T total resources, a fraction was allocated to one measured trait, $T_1 \propto R_1 = R_T(1 - P_1)$, and the remainder to other traits, $R_2 = R_T P_1$. Resources allocated to R_2 were then subdivided between traits $T_3 \propto R_3 = R_T P_1(1 - P_2)$ and $T_4 \propto R_4 = R_T P_1 P_2$. Both allocation fractions, P_1 and P_2, were restricted to values between 0 and 1 and, in our simulation, each trait depended linearly on the resources allocated to it, so that $T_n = R_n$.

Each of R_T, P_1, and P_2 was assumed to result from additive effects of multiple loci that did not affect the other two traits, so that the three traits were independently distributed. We further assumed that R_T, P_1, and P_2 were normally distributed with variances of V_R, V_{P_1}, and V_{P_2}, respectively. We assumed that changes in mean P_n did not affect V_{P_n}, so that V_{P_n} remained constant for each simulation. These assumptions are simplifications but are likely to be approximately correct if large numbers of loci influence each trait and when the allocation fractions do not approach the boundaries of 0 and 1. Because our focus was on evolutionary consequences of genetic variation in resource allocation, we did not incorporate environmental variation into our model. Genetic variances for each trait and covariances between traits were based on expected means and variances of products, and they reflected both mean allocation fractions and their variances (table 1; summarized in the next paragraph). Both de Laguerie et
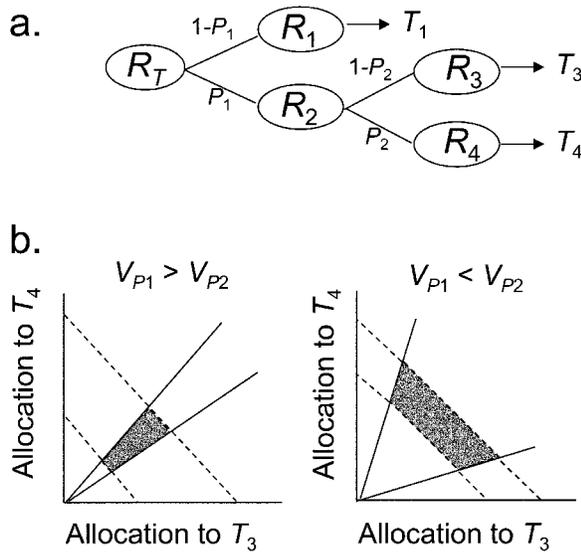
Figure 1: *a*, Two-level allocation hierarchy used in this simulation study. A fraction of the R_T total resources, $1-P_1$, is allocated to the first measured trait, $R_1 = T_1$, and the remainder, P_1 to R_2. Similarly, a fraction of the resources allocated to R_2, $1-P_2$, is allocated to the second measured trait, $R_3 = T_3$, and the remainder to the third measured trait, T_4. *b*, Graphical illustration of how different levels of variation in P_1 and P_2 affect the covariance between T_3 and T_4. The dashed lines represent the trade-off between T_3 and T_4. As allocation to R_2 increases, the trade-off lines move further from the origin because individuals can increase allocation to both T_3 and T_4. The solid lines represent relative allocation to T_3 and T_4, and the shaded areas represent the range of phenotypes within a population. In the left panel, variation in P_1 exceeds variation in P_2, so the measured relation between T_3 and T_4 is positive, despite the occurrence of a trade-off between these traits. In the right panel, variation in P_2 exceeds variation in P_1, and the measured relation between T_3 and T_4 is negative. These ideas were developed by van Noordwijk and de Jong (1986), de Laguerie et al. (1991), Houle (1991), and de Jong (1993).

al. (1991) and de Jong (1993) also considered how variances in allocation influence **G** in the presence of a hierarchy.

Allocation fractions determine mean resource allocation to each trait, and their variances determine the amount of variation around that mean. Therefore, higher values of V_{P_1} and V_{P_2} increase genetic variation in each trait. Variation in P_1 (V_{P_1}) affects variation in all traits because P_1 is at the base of the hierarchy (fig. 1*a*), whereas V_{P_2} only affects genetic variation in T_3 and T_4. The relative magnitude of V_{P_1} and V_{P_2} is the most important parameter determining the sign of the covariance between T_3 and T_4. When $V_{P_1} \gg V_{P_2}$, the covariance between T_3 and T_4 is positive because individuals with high allocation to R_2 can invest more in both T_3 and T_4 than can individuals with low allocation to R_2 (fig. 1*b*). The reverse is true when $V_{P_1} \ll V_{P_2}$. When V_{P_1} and V_{P_2} are of similar magnitude, P_1

and P_2 have a greater influence on the sign of genetic covariances. The covariance between T_3 and T_4 is more likely to be negative as P_1 increases (i.e., increasing $R_2 = R_3 + R_4 = T_3 + T_4$) and when P_2 is closer to 1.0 or 0.0 than to 0.5 (also see de Laguerie et al. 1991; fig. 3 in de Jong 1993; sample **G** matrices in the appendix).

Natural Selection

We considered two classes of fitness function. In both, we assumed an annual organism with an initial division of resources via P_1 between somatic or vegetative growth, T_1, and reproduction, $T_3 + T_4$. Somatic allocation can be thought of as influencing the probability of survival so that total fitness through vegetative and reproductive functions is multiplicative. When deriving expressions for population mean fitness, $\overline{W}$, we assumed that $V_R = 0$, so that R_T was simply a constant reflecting resource availability. We made this assumption in order to concentrate on how various combinations of V_{P_1} and V_{P_2} influenced trait evolution. Initial simulations with $V_R > 0$ resulted in almost identical direction of evolutionary change but slower rates (results not shown).

Multiplicative Fitness. In the first fitness scenario, T_3 and T_4 each contributed multiplicatively to fitness. In addition, the fitness contribution of each trait was not directly affected by the values of the other trait. Specific examples that are likely to fit this scenario include division of reproductive resources between gamete production and mate attraction or division of carbon used for vegetative growth between photosynthetic machinery and defense compounds. The fitness of individual *j* was

$$w_j = T_{1j}^{G_1} T_{3j}^{G_3} T_{4j}^{G_4},$$

$$w_i = [R_T(1 - P_{1j})]^{G_1} [R_T P_{1j}(1 - P_{2j})]^{G_3} \qquad (1)$$

$$\times (R_T P_{1j} P_{2j})^{G_4}.$$

The exponents, G_1, G_3, and G_4, described the shape of the fitness-gain curves associated with increased allocation to each trait. For example, when $G_1 < 1$, fitness gain through increased allocation to T_1 was decelerating, whereas when $G_1 > 1$, the equivalent fitness gain was accelerating. Following Lande (1979), population mean fitness was described by

$$\overline{W} = \int \int \int w \cdot f(T_1)f(T_3)f(T_4)\partial T_1 \partial T_3 \partial T_4, \qquad (2)$$

where $f(x)$ is a function describing the normal probability distributions for each trait. We were unable to obtain an

Table 1: Formulas used to calculate variation within and covariation between the three measurable traits, T_1, T_3, and T_4

	T_1	T_3	T_4
T_1	$R_T^2 V_{P_1} + \left(1 - \overline{P_1}\right)^2 V_R + V_R V_{P_1}$	$\left(1 - \overline{P_2}\right)\left\{-R_T^2 V_{P_1} + \left[\overline{P_1}\left(1 - \overline{P_1}\right)V_R\right] - V_R V_{P_1}\right\}$	$\overline{P_2}\left\{-R_T^2 V_{P_1} + \left[\overline{P_1}\left(1 - \overline{P_1}\right)V_R\right] - V_R V_{P_1}\right\}$
T_3		$\left(R_T^2 + V_R\right)\left(\overline{P_1}^2 + V_{P_1}\right)\left[\left(1 - \overline{P_2}\right)^2 + V_{P_2}\right] - R_T^2 \overline{P_1}^2\left(1 - \overline{P_2}\right)^2$	$\left(R_T^2 + V_R\right)\left(\overline{P_1}^2 + V_{P_1}\right)\left[\overline{P_2}\left(1 - \overline{P_2}\right) + V_{P_2}\right]$ $- R_T^2 \overline{P_1}^2 \overline{P_2}\left(1 - \overline{P_2}\right)$
T_4			$\left(R_T^2 + V_R\right)\left(\overline{P_1}^2 + V_{P_1}\right)\left(\overline{P_2}^2 + V_{P_2}\right) - R_T^2 \overline{P_1}^2 \overline{P_2}^2$

Note: See figure 1. R_T represents total resource status, P_1 represents allocation of R_T between R_1 and R_2, and P_2 represents allocation of R_2 between T_3 and T_4; V refers to the population-level variances in resource status and allocation fractions. The formulas were derived by Bohrnstedt and Goldberger (1969) and are similar to those used by de Jong (1993).

analytical solution for this expression when G_1, G_3, and $G_4 \neq 1$. Therefore, we obtained an approximate expression for $\overline{W}$ using a third-order Taylor expansion for equation (1) around the trait means, $\overline{T_1}$, $\overline{T_3}$, and $\overline{T_4}$. Although we could not test the accuracy of the expression obtained directly, a similar expression obtained for $G_1 = G_3 = G_4 = 1.0$ was obtained through both integration and the Taylor expansion. When these expressions were both used to calculate $\overline{W}$, the Taylor expansion was accurate to within 10^{-6}% of the true value.

The vector of partial selection gradients, Lande's (1979) gradient operator $\nabla \ln W = \boldsymbol{\beta}$, was obtained by taking partial derivatives of $\overline{W}$ (as estimated by the Taylor series) with respect to changes in trait means:

$$\boldsymbol{\beta}_{T_1} = \frac{\partial \overline{W}}{\partial \overline{T_1}},$$

$$\boldsymbol{\beta}_{T_3} = \frac{\partial \overline{W}}{\partial \overline{T_3}}, \tag{3}$$

$$\boldsymbol{\beta}_{T_4} = \frac{\partial \overline{W}}{\partial \overline{T_4}}.$$

Additive, Frequency-Dependent Fitness. The second scenario we considered is one in which hermaphroditic individuals allocated reproductive resources between gametes that were female, T_3, or male, T_4. Here we included terms to account for the frequency-dependent nature of selection on reproductive allocation. In general, population mean fitness must be equal through male and female function because every individual has a mother and a father (Charnov 1982). If male fertility is limited primarily by access to female gametes (cf. Bateman 1948) and female fertility by production of female gametes (here T_3) that all become offspring, then $\overline{W} = 2\overline{W}_{T_3}$. The following expression (Charlesworth and Charlesworth 1981; Lloyd 1984;

Charlesworth and Morgan 1991) describes the fitness of hermaphroditic individual j:

$$w_j = w_{T_3 j} + w_{T_4 j},$$

$$w_j = T_{1j}^{G_1} T_{3j}^{G_3} + T_{1j}^{G_1} T_{4j}^{G_4}\left(\frac{\overline{W}_{T_3}}{\overline{W}_{T_4}}\right). \tag{4}$$

Thus, fitness gain through male function depends on an individual's relative contribution to the male gamete pool, $T_{4j}/\overline{W}_{T_4}$, and on the availability of female gametes for fertilization, $\overline{W}_{T_3}$. In this scenario, $\overline{W}_{T_4}$ represents potential male fitness through gamete production rather than male fitness per se, which by definition equals $\overline{W}_{T_3}$.

Once again, following Lande (1979), population mean female and male gamete production was described by

$$\overline{W}_{T_3} = \int \int w_{T_3} \cdot f(T_1)f(T_3)\partial T_1 \partial T_3,$$

$$\overline{W}_{T_4} = \int \int w_{T_4} \cdot f(T_1)f(T_4)\partial T_1 \partial T_4, \tag{5}$$

where $f(x)$ is a function describing the normal probability distributions for each trait. As before, we used Taylor expansions to obtain expressions for these integrals. In this case, the selection gradients for female and male fitness were

$$\boldsymbol{\beta}_{T_1} = \frac{\partial \overline{W}_{T_3}}{\partial \overline{T_1}} + \frac{\partial \overline{W}_{T_4}}{\partial \overline{T_1}} \times \frac{\overline{W}_{T_3}}{\overline{W}_{T_4}},$$

$$\boldsymbol{\beta}_{T_3} = \frac{\partial \overline{W}_{T_3}}{\partial \overline{T_3}}, \tag{6}$$

$$\boldsymbol{\beta}_{T_4} = \frac{\partial \overline{W}_{T_4}}{\partial \overline{T_4}} \times \frac{\overline{W}_{T_3}}{\overline{W}_{T_4}}.$$

The additional term, $\overline{W}_{T_3}/\overline{W}_{T_4}$, reflects the fact that the advantage of a change in male allocation should depend on the availability of female gametes relative to the mean production of gametes by competitors.

Artificial Selection

In order to assess how hierarchical allocation affects responses to artificial selection, we assumed an experiment in which one trait was exposed to truncation selection. Predicting the effects of selection on all three traits was straightforward because we assumed all phenotypic variation to reflect genes of additive effect. Therefore, following Falconer and Mackay (1996), the selection differential for selected trait x could be predicted from i, the intensity of selection:

$$S_x = i\sqrt{V_{\mathrm{p}x}} = i\sqrt{V_{\mathrm{a}x}}, \tag{7}$$

where p refers to phenotypic and a to additive genetic variation. In general, the correlated selection differential, S'_y, on trait y through selection on x is

$$S'_y = b_{\mathrm{p}yx}S_x, \tag{8}$$

where $b_{\mathrm{p}yx}$ describes the phenotypic correlation between y and x. Here, all variation was additive genetic so that $b_{\mathrm{p}yx} = b_{\mathrm{a}yx} = r_{\mathrm{a}}(V_{\mathrm{a}y}/V_{\mathrm{a}x})^{0.5}$. Substituting this expression and equation (7) into equation (8) yields

$$S'_y = r_{\mathrm{a}}\sqrt{\frac{V_{\mathrm{a}y}}{V_{\mathrm{a}x}}}i\sqrt{V_{\mathrm{a}x}} = r_{\mathrm{a}}i\sqrt{V_{\mathrm{a}y}},$$

$$S'_y = \frac{\mathrm{Cov}_{xy}}{\sqrt{V_{\mathrm{a}y}V_{\mathrm{a}x}}}i\sqrt{V_{\mathrm{a}y}} = i\frac{\mathrm{Cov}_{xy}}{\sqrt{V_{\mathrm{a}x}}}. \tag{9}$$

Thus, the effects of direct selection on each trait are given by equation (7) and indirect selection due to correlated traits by equation (9). These effects were summed to estimate the total selection gradient acting on each trait. Predicting the multivariate selection response, R, was made straightforward by the assumptions that all variation was genetic and that all natural selection was suspended:

$$R = G\beta = GP^{-1}S = GG^{-1}S = S, \tag{10}$$

where P^{-1} is the matrix of phenotypic variances and covariances and S is the vector of selection differentials.

Simulations and Results

General Approach to Simulations

We investigated how genetic variation in allocation fractions, V_{P_1} and V_{P_2}, influenced responses to natural and artificial selection. To simulate response to natural selection, we set population-mean allocation fractions at starting values differing from the optimal allocation. This scenario is analogous to a population occupying a new or altered environment. The response to selection in each generation was approximated as $R = G\beta$. This approximation ignores gametic disequilibria and any interactions among loci introduced by the multiplicative action of allocation genes (de Jong and van Noordwijk 1992; Dillmann and Foulley 1998). However, the error introduced by these effects is small when the variances are small, as in our simulations. Both G and β were recalculated each generation because genetic variances and covariances among traits and selection gradients depend on allocation fractions. Genetic variation in the allocation fractions, V_{P_1} and V_{P_2}, was assumed to remain constant during each simulation, and the simulations were run for enough generations to allow populations to reach optimal allocation; that is, all trait means remained constant. For each set of starting allocation, optimal allocation, and selection regime, we compared rate and direction of evolution for three combinations of V_{P_1} and V_{P_2}. These were $V_{P_1} = 10 \times V_{P_2}$, $V_{P_1} = V_{P_2}$, and $10 \times V_{P_1} = V_{P_2}$. We use the term "variance ratio," or $V_{P_1} : V_{P_2}$, to refer to the magnitude of V_{P_1} relative to V_{P_2}. Thus, variance ratios examined were $V_{P_1} : V_{P_2} = 0.1, 1,$ and 10.

To investigate how genetic variation in allocation fractions affects responses to artificial selection, we assumed truncation selection on a single trait, either T_3 or T_4. We assumed that all natural selection was suspended, which was equivalent to assuming that selected individuals had equal viability and fecundity. Starting allocations were as for natural selection. As for natural selection, we compared rate and direction of evolution for different combinations of V_{P_1} and V_{P_2}. We chose values of V_{P_1} and V_{P_2} that resulted in zero or positive correlations between traits T_3 or T_4 in order to simulate situations in which quantitative-genetic correlations would not reflect the trade-off between T_3 and T_4. These varied from $0.7 \times V_{P_1} = V_{P_2}$ to $10 \times V_{P_1} = V_{P_2}$.

Natural Selection

Direction of Evolution. We examined the effects of variance ratios ($V_{P_1} : V_{P_2}$) on the evolution of T_1, T_3, and T_4 for 16 scenarios (table 2). Responses to selection were compared for two starting allocation patterns ("Start point" in table 2), and traits contributed to fitness either additively or multiplicatively. Optimal allocation patterns depend on the

Table 2: Gain curve parameters for the 16 scenarios used to test the effects of variance ratio $(V_{P_1} : V_{P_2})$ on the evolution of traits involved in hierarchies

	Start point			
	$T_1 = 6,\ T_3 = 1.2,\ T_4 = 2.8$		$T_1 = 4,\ T_3 = 4.2,\ T_4 = 1.8$	
Fitness	Additive	Multiplicative	Additive	Multiplicative
Gain curve:				
1	.5, 1.0, 1.0 (fig. 2*a*)	.5, 1.0, 1.0 (fig. 2*b*)	.5, 1.0, 1.0	.5, 1.0, 1.0
2	.5, 1.5, .5 (fig. 2*c*)	.5, 1.5, .5 (fig. 2*d*)	.5, 1.5, .5	.5, 1.5, 1.5
Optimum:				
1	1.0, .5, .5 (fig. 3*a*)	1.5, .4, .4 (fig. 3*b*)	1.0, .5, .5	1.5, .4, .4
2	1.0, 1.0, .5 (fig. 3*c*)	1.5, .5, .25 (fig. 3*d*)	1.0, 1.0, .5	1.5, .5, .25

Note: Two combinations of initial allocation to T_1, T_3, and T_4 (start points) were tested. T_3 and T_4 contributed either additively or multiplicatively to fitness. Gain curve parameters, G_1, G_3, and G_4, for each of the three traits determine the optimal allocation pattern. The two sets of gain curves specified in the top half of the table were the same for additive and multiplicative fitness but did not necessarily yield the same optima. The gain curve parameters in the bottom half of the table were chosen to yield similar optima for additive and multiplicative fitness. Figure number and panel showing the simulation results for the first start point are given in parentheses.

gain curve parameter for each trait, G_1, G_3, and G_4, and on how traits contribute to fitness. In eight of the scenarios tested, gain curve parameters were identical for additive and multiplicative fitness, a situation that did not necessarily yield the same optimal allocation pattern (table 2, top half). In the remaining eight scenarios, gain curve parameters were chosen to yield a similar optimum for additive and multiplicative fitness (table 2, bottom half). For each combination of starting point, selection regime, and gain curves, we compared the direction of evolution for variance ratios of $V_{P_1} : V_{P_2} = 10$, 1, and 0.1. The values of V_{P_1} and V_{P_2} were 0.0003 or 0.003 and resulted in evolvability values from 0.08% to 5%, where evolvability = $(V_{T_n}/\overline{T}_n^2) \times 100\%$ (Houle 1992).

As was predictable from changes in **G** (see "Hierarchical Allocation and Genetic Variation" and appendix), differences in the variance ratio had large effects on the direction of evolution (figs. 2, 3). In these figures, evolutionary changes perpendicular to the trade-off line correspond to evolution of P_1, whereas evolution of P_2 is represented by changes parallel to the trade-off line, that is, changes in relative allocation to T_3 versus T_4. The general effects of variance ratio were similar for all combinations tested and therefore are shown only for the first starting allocation in table 2. Initial evolutionary change was in the allocation fraction with the most variation, even if this meant the population initially evolved to a position more distant from the overall optimum than the starting point (figs. 2, 3).

The effects of variance ratio on trait evolution are detailed below. When the variance ratio was 10, indicating a V_{P_1} 10 times that of V_{P_2}, initial change was primarily toward optimal P_1 so that T_3 and T_4 either both increased or both decreased, even if selection favored increases in

one trait and decreases in the other (e.g., fig. 2*c*). Conversely, when the variance ratio was 0.1, initial change was primarily toward the optimal P_2, and the trade-off between T_3 and T_4 was immediately apparent from an increase in one trait and a decrease in the other (fig. 2). A variance ratio of 1 resulted in an intermediate trajectory. This general pattern held for both multiplicative and additive (frequency-dependent) selection, contrasting gain curve parameters (fig. 2), contrasting optima (fig. 3), and both starting points. However, it was less striking when the starting point and optimum differed mostly in one allocation fraction and not the other, so that most change was either parallel or perpendicular to the trade-off line (e.g., fig. 3*c*, 3*d*).

Exact evolutionary trajectories depended on selection regime, starting point, and gain curves. Identical gain curve parameters often led to different optima for multiplicative and additive selection and corresponding differences in evolutionary pathways (fig. 2). When gain curves were chosen to yield similar optima, the pathways to a given optimum differed slightly between selection regimes, with populations under multiplicative selection generally evolving more directly to the optimum (fig. 3). However, these differences did not alter the fact that high variance ratios masked the trade-off between T_3 and T_4 from initial responses to selection, whereas low variance ratios resulted in initial selection responses consistent with a trade-off.

Rate of Evolution. Rates of evolutionary change are illustrated by plotting population mean allocation every 10 generations (figs. 2, 3). These rates depended on genetic parameters, **G**, and on the strength of selection. The effects of V_{P_1} and V_{P_2} on initial rates of change can be seen by
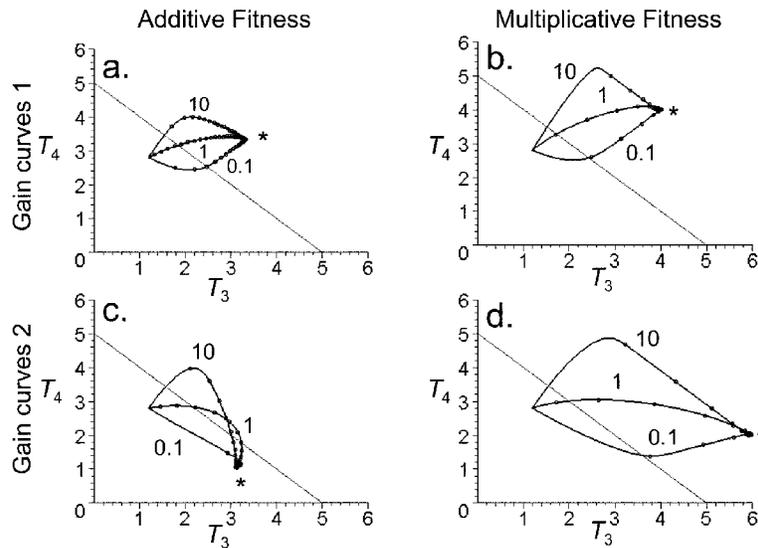
Figure 2: Evolutionary trajectories for contrasting fitness and gain curve parameters. In each plot, the straight line represents the trade-off between T_3 and T_4 when resources are evenly allocated between R_1 and R_2 ($P_1 = 0.5$). Evolutionary changes in P_1 are perpendicular to the trade-off line, and evolutionary changes in P_2 are parallel to the trade-off line. Each simulation was conducted for variance ratios ($V_{P_1} : V_{P_2}$) of 10, 1.0, and 0.1 and for the same starting allocation. Optimal allocations were determined by the gain curve parameters in table 2 and are indicated with asterisks. Symbols were plotted every 10 generations.

comparing rates of change among variance ratios. For example, V_{P_1} was the same for the ratio 1 ($V_{P_1} : V_{P_2} = 1 : 1$) and 0.1 ($V_{P_1} : V_{P_2} = 1 : 10$). Consequently, initial change in P_1, that is, change perpendicular to the trade-off line, was similar (fig. 2d; fig. 3a, 3b; cf. position of symbols for variance ratios of 1 and 0.1). Similarly, initial change in P_2, that is, change parallel to the trade-off line, was similar for variance ratios of 10 ($V_{P_1} : V_{P_2} = 10 : 1$) and 1. Slight differences reflected contrasting selection pressures on populations at different allocations and evolutionary changes in **G**. The strength of selection was governed by gain curves and the distance between the population mean and optimal allocation, with larger gain-curve parameters and larger distances corresponding to stronger selection. In addition, evolution under additive selection was slower, even when populations evolved to similar optima (fig. 3).

Time to Trade-Off. Whether or not trade-offs between T_3 and T_4 are reflected in negative genetic correlations depends on allocation fractions and their variances (see "Hierarchical Allocation and Genetic Variation"). We were interested in how changes in variance ratio ($V_{P_1} : V_{P_2}$) affect the time until trade-offs are apparent from the selection response, particularly in cases where the covariance between T_3 and T_4 was not negative. Trade-offs were considered apparent in the generation that T_3 and T_4 responded in opposite directions to selection, that is, one trait increased and the other decreased. Both differences

in the absolute amount of genetic variation and differences in variance ratio will affect rates of evolution and therefore the time until trade-offs are evident. We considered three values for V_{P_1}: 0.003, 0.00165, and 0.0003. For each V_{P_1}, we altered V_{P_2} to obtain variance ratios ranging from 0.1 to 10 and measured the number of generations until T_3 and T_4 responded in opposite directions to selection.

We examined the effects of the variance ratio on the number of generations until a trade-off was apparent for the 16 scenarios investigated above (table 2). The results fell into two general patterns. In the first category (fig. 4), trade-offs always became evident eventually because the difference between the starting point and optimum primarily involved change in opposite directions for T_3 and T_4 (e.g., figs. 2c, 3). In our example of additive fitness, variance ratios <0.7 caused T_3 to increase immediately and T_4 to decrease so that the trade-off between these traits was apparent in the first generation of selection (fig. 4a). The number of generations before the trade-off between T_3 and T_4 was apparent increased with variance ratios >0.7. This increase was sharper when V_{P_1} was low than when V_{P_1} was high (fig. 4). Low values of V_{P_1} meant that populations had lower genetic variation overall and that they evolved more slowly along the same trajectory. As a result, it took more generations for T_3 and T_4 to begin evolving in opposite directions. These patterns were very similar for multiplicative fitness (fig. 4b).

In the second category (fig. 5), trade-offs were only
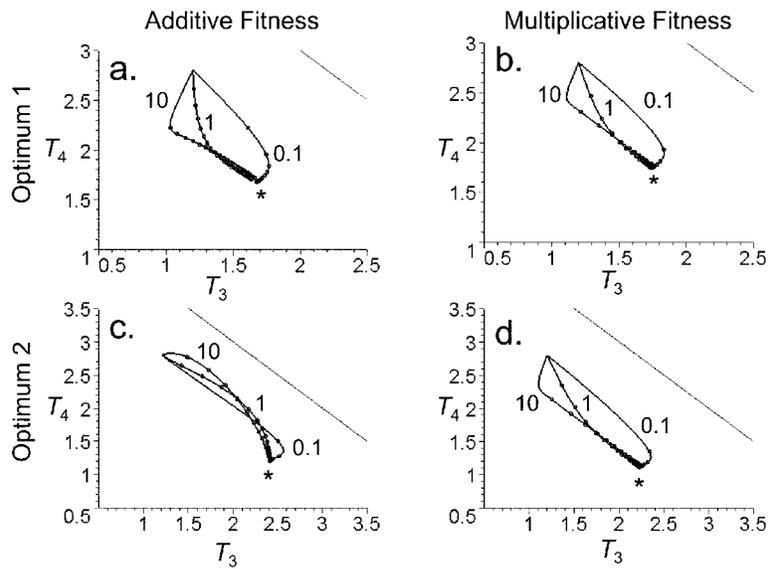
Figure 3: Evolutionary trajectories for contrasting fitness parameters and optimal allocation patterns. In each plot, the straight line represents the trade-off between T_3 and T_4 when resources are evenly allocated between R_1 and R_2 ($P_1 = 0.5$). Evolutionary changes in P_1 are perpendicular to the trade-off line, and evolutionary changes in P_2 are parallel to the trade-off line. Each simulation was conducted for variance ratios ($V_{P_1} : V_{P_2}$) of 10, 1.0, and 0.1 and for the same starting allocation. Optimal allocations were determined by the gain curve parameters in table 2 and are indicated with asterisks. Symbols were plotted every 10 generations.

sometimes evident from the selection response because the difference between the starting point and optimum primarily involved change in the same direction for T_3 and T_4 (e.g., fig. 2a, 2b). When fitness was additive, variance ratios between 0.4 and 0.55 caused both T_3 and T_4 to increase throughout the simulation, and the trade-off between T_3 and T_4 never became evident (fig. 5a). However, variance ratios <0.4 caused T_3 to increase immediately and T_4 to decrease so that the trade-off between these traits was apparent in the first generation of selection (fig. 5a). Variance ratios >0.55 initially caused both T_3 and T_4 to increase, but the trajectory was indirect so that eventually one trait had to decrease and the other increase for the population to reach the optimum (fig. 2a, 2b). Once again, these patterns were qualitatively similar for multiplicative fitness (fig. 5b).

Artificial Selection

We examined four scenarios to investigate how allocation hierarchies and variance ratios affect responses to artificial selection. We assumed selection on a single trait, either T_3 or T_4, and used the same two starting values examined for natural selection. For each of the four combinations, we chose two values for V_{P_2} (0.000165 and 0.0003). We then altered V_{P_1} to obtain variance ratios ranging from 0.7 to 10. The lowest value resulted in a near zero correlation

between T_3 and T_4, whereas the highest resulted in a large positive correlation. Thus, most variance ratios were high enough to cause a positive genetic correlation between T_3 and T_4 and to mask the trade-off between these traits. We measured responses to selection and the number of generations until a trade-off was evident at $i = 1.554$. This intensity corresponds to truncation selection on the upper 15% of the population.

Responses to artificial selection followed the same general patterns for the two different starting points, whether selection was on T_3 or T_4, and for different overall levels of genetic variation (figs. 6, 7). Variance ratios had qualitative effects on evolutionary trajectories that were similar to those described above for natural selection. Lower variance ratios resulted in evolution parallel to the trade-off line, that is, one trait decreased and the other increased for most of the simulation. At higher variance ratios, evolutionary increases in both traits remained inconsistent with trade-offs for many generations, although the evolutionary trajectory eventually changed to a direction closer to the trade-off line (fig. 6). Depending on how long selection was carried out, the joint evolution of T_3 and T_4 could give the impression that these traits were either genetically uncorrelated or positively correlated. In our example, rates of evolution were faster with higher variance ratios because these variance ratios were achieved through an increase in V_{P_1} while holding V_{P_2} constant.
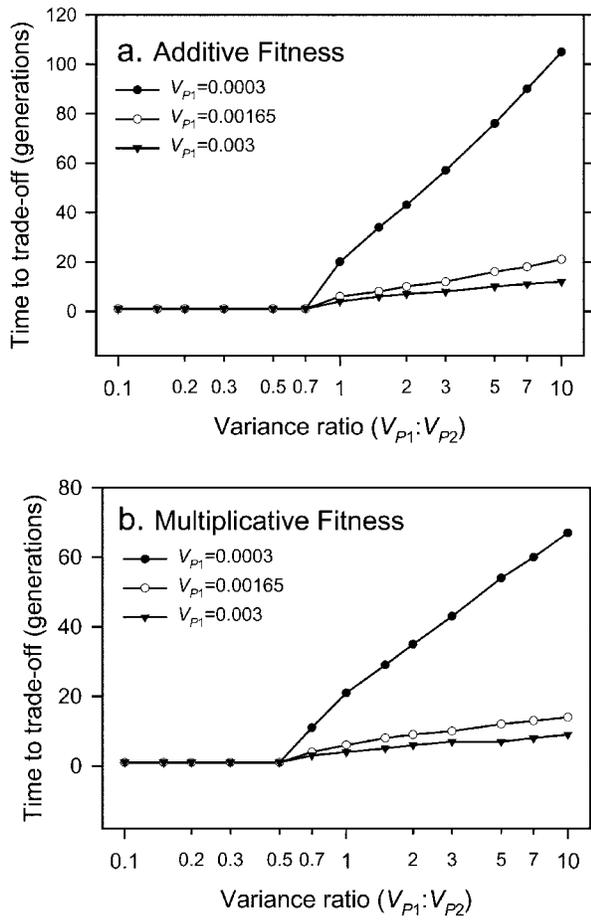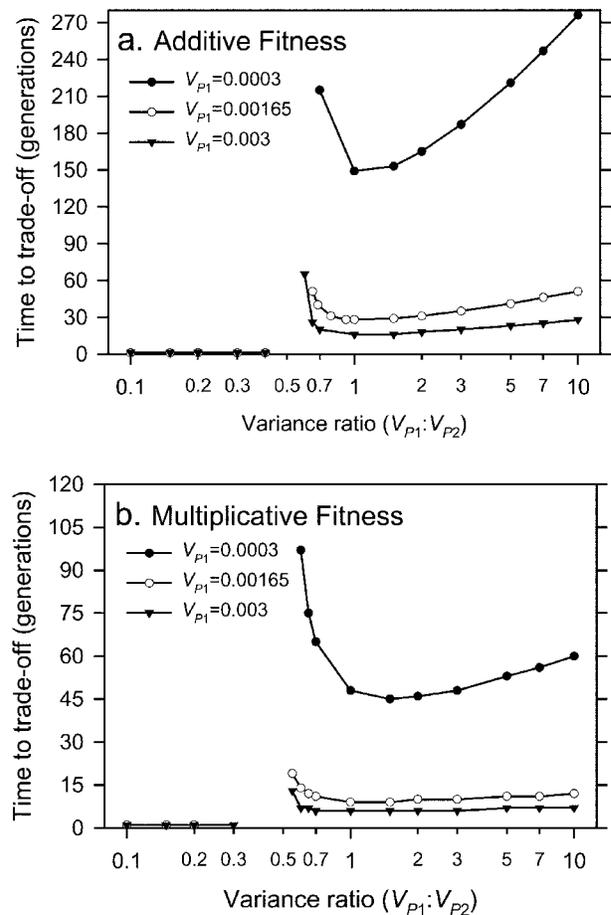
Figure 4: Number of generations until a trade-off between T_3 and T_4 was apparent from increases in one trait and decreases in the other for simulations in which the trade-off always became apparent. The effects of changes in variance ratio ($V_{P_1} : V_{P_2}$) are shown for three values of V_{P_1}. *a*, Times corresponding to the simulation shown in figure 2*c*. *b*, Times corresponding to the simulation shown in figure 2*d*.

As for natural selection, greater variance ratios increased the number of generations before a trade-off was apparent from evolution of T_3 and T_4 (fig. 7). These increases occurred even though overall genetic variation, and rate of evolution, was greater for higher variance ratios. In our examples, trade-offs were generally evident within 20 generations when variance ratios were <3 and sometimes within five generations. More generations of selection would be required to reveal trade-offs in the presence of higher variance ratios. Thus, while it is possible for artificial selection to reveal trade-offs that were not apparent from **G**, this is not ensured within the time frame of many experiments. Moreover, the rate of evolution may have been unrealistically high in our simulation because physical limitations on trait values were not incorporated into

our models, and genetic variation for the traits in question was assumed to remain high even after several generations of strong selection.

Discussion

This study indicates how allocation hierarchies may affect the direction and rate of evolutionary change in life-history traits. We assumed that resources were allocated in a simple two-level hierarchy and that **G** depended on allocation fractions at each level of the hierarchy and their genetic variances. Simulated responses to selection indicated that


Figure 5: Number of generations until a trade-off between T_3 and T_4 is apparent from increases in one trait and decreases in the other for simulations in which trade-offs did not necessarily become apparent from the selection response. The effects of changes in variance ratio ($V_{P_1} : V_{P_2}$) are shown for three values of V_{P_1}. *a*, Times corresponding to the simulation shown in figure 2*a*. When variance ratios were between 0.4 and 0.55, trade-offs were never evident. *b*, Times corresponding to the simulation shown in figure 2*b*. Trade-offs were not evident when variance ratios were between 0.3 and 0.5.

a. Starting point 1, selection on T_3
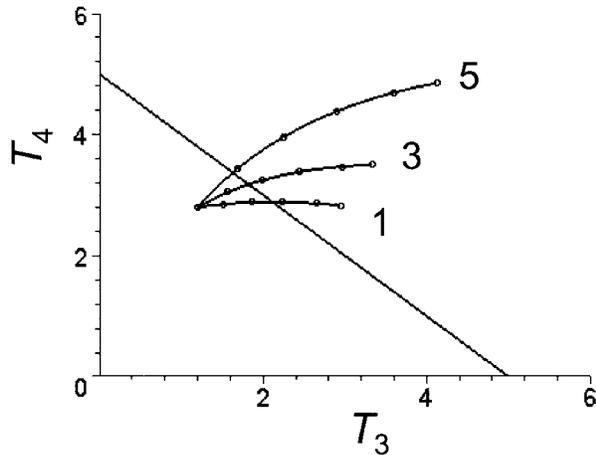
## b. Starting point 2, selection on T_4
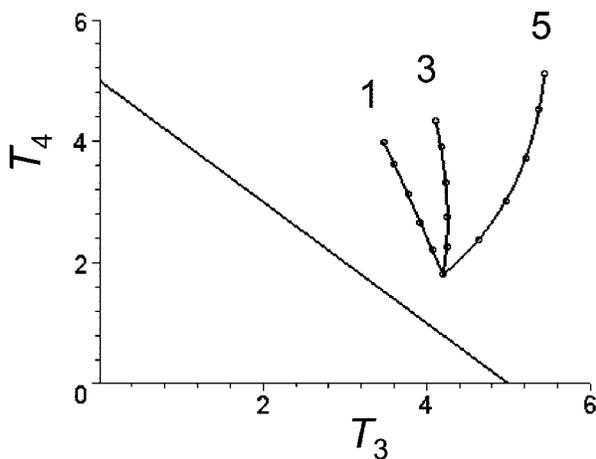
Figure 6: Direct and correlated responses to artificial selection for (*a*) increased T_3 and (*b*) increased T_4 for variance ratios of 1, 3, and 5. Symbols are plotted every three generations. Starting points 1 and 2 correspond to those shown in table 2.

evolutionary changes in traits that competed for resources were often inconsistent with trade-offs. Specifically, traits that used a common resource at the end of an allocation hierarchy frequently responded to selection with simultaneous increases or decreases in each trait mean, despite the presence of a trade-off between them. We discuss the implications of these findings and consider empirical data relevant to hierarchical allocation, limitations of the model, and directions for future research.

We primarily focus on two examples of a reproductive hierarchy in which resources invested in reproduction are subdivided either between offspring size and number or between female and male function. This approach allows us to discuss relevant empirical evidence in some detail. Of course, many other allocation hierarchies are possible. Other components of reproductive allocation that may compete for resources include gametes, secondary sexual characters, parental care, and mate attraction. Other components of somatic allocation include foraging, photosynthesis, defense mechanisms, current growth, and future growth.

Direction and Rate of Evolution

Rates of evolution depend largely on the genetic variation available for selection to act on. Therefore, evolution is
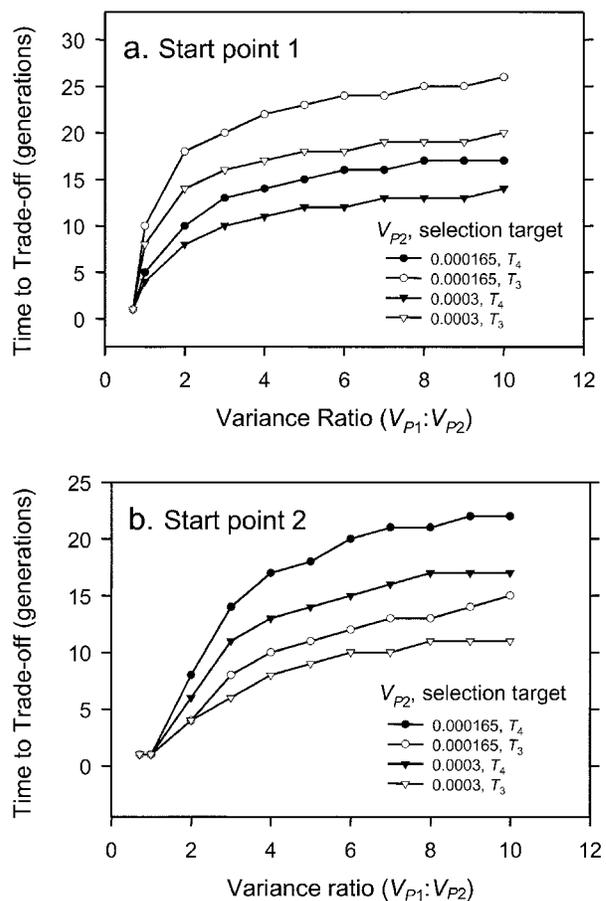
Figure 7: Number of generations until a trade-off between T_3 and T_4 is apparent from responses to artificial selection that are in opposite directions. *a*, Times corresponding to the simulation shown in figure 6*a*. *b*, Times corresponding to the simulation shown in figure 6*b*. In both panels, the effects of changes in variance ratio ($V_{P_1} : V_{P_2}$) are shown for two values of V_{P_2} and for selection on T_3 and T_4.

expected to proceed most rapidly in directions with ample genetic variation (Via and Lande 1985; Schluter 1996, 2000). In our model of hierarchical allocation, when variation in one allocation fraction far exceeded variation in the other, initial evolutionary change was mainly in the variable allocation step. Although trait values were always constrained by both trade-offs in the hierarchy, one trade-off essentially masked the other when variances were very unequal. These qualitative patterns probably apply fairly generally because they were robust to differences in selection regimes, starting points, and optima.

Whether and when trade-offs became apparent from responses to selection depended on both the ratio of allocation variances and the direction of selection. Variance ratios primarily determined when trade-offs became apparent. Hierarchical allocation masked trade-offs from initial responses to selection when variation in allocation at the base of the hierarchy equaled or exceeded that further along the hierarchy. This condition may often occur in natural populations. For example, many factors contribute to genetic variation in overall allocation to reproduction. Fecundity increases at the expense of longevity in fruit flies *Drosophila* (e.g., Zwaan et al. 1995), and life span varies negatively with the frequency of mating opportunities, as determined by fruit abundance, among 18 species in Panama (Sevenster and van Alphen 1993). Similarly, fecundity is negatively correlated with the ability to resist parasites in *Drosophila melanogaster* (Fellows et al. 1999), and resistance levels vary widely across Europe (Kraaijeveld and Godfray 1999). In these examples, populations contain substantial genetic variation for longevity or parasite resistance and therefore in allocation to reproduction. This variation may be sufficient to mask trade-offs among components of reproduction from comparisons of diverging populations. Similar situations seem likely to apply to other taxa.

Although extreme variance ratios delayed the effects of trade-offs in the selection response, they did not necessarily mask trade-offs indefinitely. However, the direction of selection may prevent a trade-off from ever becoming apparent. In hindsight, this is intuitively obvious. If a selection gradient favors a simultaneous increase in a pair of traits that are subject to a trade-off, both traits will increase, and the trade-off between them will never be apparent from responses to selection or from comparisons of populations at evolutionary equilibrium. How likely is this situation to affect the evolution of natural populations?

This question may be illuminated by considering the evidence for specific trade-offs. One example is female versus male function in hermaphroditic organisms. The evidence for a trade-off between female and male allocation in plants comes largely from comparisons within dimorphic populations, in which individuals of each morph exhibit gender specialization (Goldman and Willson 1986). However, few negative genetic correlations between female and male investment have been detected in species with hermaphroditic individuals (review in Mazer et al. 1999). De Laguerie et al. (1991) proposed hierarchical allocation as a potential explanation for this pattern. Mazer and Delesalle (1998) predicted that variation in sex allocation should be low in autonomously selfing species because flowers produce only enough pollen to fertilize their own ovules, introducing a positive correlation between pollen and ovule production. This reasoning suggests that comparative studies involving selfing species would not reveal a trade-off between female and male allocation. Thus, in some situations, neither within-population variation in allocation nor among-population comparisons will reveal life-history trade-offs.

Our simulations of artificial selection hold both encouragement and a cautionary note for the experimentalist interested in detecting negative genetic correlations. When variance ratios were comparable, artificial selection revealed trade-offs within 10 generations (figs. 6, 7). Thus, selection on species with short generation times may reveal masked trade-offs. In some cases, artificial selection has revealed trade-offs even more quickly. For example, trade-offs between female and male allocation in *Spergularia marina* (Mazer et al. 1999), between flower size and number in *Silene latifolia* (Meagher 1994) and *Eichhornia paniculata* (Worley and Barrett 2000), and between pollen grain size and number in *Brassica rapa* (Sarkissian and Harder 2001) were revealed after only two or three generations of artificial selection. However, trade-offs may be less easily revealed through artificial selection when variance ratios are high, and even 10 generations exceeds the duration of most selection experiments. Furthermore, our results will not apply directly to experiments that do not control for aspects of natural selection such as variation in fecundity and viability. Indeed, seven generations of artificial selection on egg size in *D. melanogaster* did not reveal a trade-off between egg size and number (Schwarzkopf et al. 1999), even though comparative and phenotypic studies attest to the general significance of trade-offs between size and number (e.g., Roff 1992; Vonhof and Harder 1995; Worley and Barrett 2000; Worley et al. 2000; Leishmann 2001). Thus, artificial selection will not always reveal important life-history trade-offs.

In general, our results emphasize the importance of considering how resources might be allocated among traits. In particular, researchers should consider allocation events that might precede the trade-off in which they are interested. They could then either control for this variation experimentally, in their choice of populations or species for comparative studies, or measure how much it influences the correlation between the traits that are of primary

interest (see also de Laguerie et al. 1991; Koelewijn and Hunscheid 2000; Worley and Barrett 2001).

Evidence for Hierarchical Allocation

Although existing data can be interpreted in terms of hierarchical allocation, virtually no studies have examined hierarchies explicitly. Thus, it is unclear whether the patterns of resource allocation and genetic variation modeled in our two-level hierarchy capture those in real organisms. This question may be addressed using classical quantitative genetics as well as other approaches aimed at identifying the number and action of genes influencing allocation patterns.

The modular construction of plants makes allocation hierarchies particularly easy to identify. For example, most species produce multiple inflorescences with numerous flowers, each producing many gametes (Venable 1996). Quantitative-genetic analysis of two populations of the tropical herb *Eichhornia paniculata* supported the occurrence of trade-offs between size and number of flowers produced per inflorescence and between inflorescence size and number. However, high genetic variation in investment per inflorescence often caused positive genetic correlations between flower size and number (Worley and Barrett 2001). To our knowledge, this is the first study to examine variation in the components of a proposed hierarchy.

Although traditional quantitative-genetic measurements provide some support for allocation hierarchies, they do not identify the genes controlling allocation within hierarchies. The ability to map quantitative trait loci (QTL) allows researchers to estimate how many genes affect individual traits and the frequency of pleiotropic effects on other traits (Mitchell-Olds 1995; Jones et al. 1997). In maize, for example, QTL affecting yield components (ear number, ear size, kernel mass and depth) suggest the presence of genes affecting overall investment in seeds and of others governing relative allocation among components of seed production (Veldboom and Lee 1996). QTL studies on *Arabidopsis thaliana* indicate a similar hierarchy (Mitchell-Olds 1996; Alonso-Blanco et al. 1999). As QTL studies accumulate, comparing both the number of genes influencing allocation within hierarchies and the magnitude of genetic variation at each level should become feasible.

Another approach to characterizing hierarchies may be to consider the physiology underlying patterns of resource allocation, as has been done for wing polymorphic insects (Zera and Denno 1997; Zera and Harshman 2001). In polymorphic species, short-winged females mature faster and produce larger, heavier ovaries than do long-winged females. These differences reflect a genetically based trade-off between reproduction and dispersal ability (Zera and Mole 1994; Stirling et al. 2001), which is mediated through juvenile hormone (JH; Zera and Harshman 2001). JH also enhances ovarian growth and reduces wing and flight muscles in some nonpolymorphic species (Nijhout 1994). Thus, genes regulating JH influence reproductive allocation in insects, and variation in these genes may affect relationships among components of reproduction such as egg size and number. Hence, genes affecting JH may correspond to genes at the first level of a hierarchy involving reproductive allocation.

Realism of the Model and Future Research

In the model presented here, variance ratios profoundly affected both **G** and evolutionary trajectories (figs. 2, 3). However, many questions remain about the nature of real hierarchies. How many loci influence allocation fractions, and what is their mode of action? Is genetic variation in allocation at the base of hierarchies generally higher than, similar to, or lower than variation near the tips? Is the genetic variation in allocation fractions likely to remain constant over evolutionary time, as is assumed here (see de Jong and van Noordwijk 1992 and Dillmann and Foulley 1998 for more explicit models of multiplicative gene action)? How does the dynamic nature of resource allocation affect hierarchies, **G** matrices, and evolution? We consider these questions and suggest possibilities for future research.

Answering the first two questions clearly requires empirical study. Information from studies of QTL and biosynthetic pathways needs to be translated into **G** matrices and selection responses. One possibility is to generate artificial populations using model organisms, such as *A. thaliana* and *D. melanogaster*, with known variance ratios for the hierarchy of interest. Artificial selection on these populations could be used to test the predictions presented here. For example, responses to selection on offspring size and number could be compared in *D. melanogaster* lines with high and low genetic variation in fecundity. Alternatively, researchers could conduct similar studies using natural populations with contrasting variation in allocation at different levels of a hierarchy. For example, species with clonal propagation may vary more in allocation to sexual reproduction than aclonal species. Indeed, genetic variation in clonal versus sexual allocation has been demonstrated in several plants and animals (Ceplitis 2001). Thus, relative variation in allocation to components of reproduction (e.g., female vs. male) may be higher in nonclonal species, even if absolute variation is comparable, making it easier to detect trade-offs among such components.

Finally, these allocation models assumed that allocation occurs only once within each generation and therefore did

not incorporate the dynamic nature of resource allocation. Many aspects of resource allocation are adjusted according to feedback from environmental stimuli. For example, investment in seeds and fruit often reduces further flower and gamete production (Silvertown 1987; Diggle 1993). Production of many costly secondary compounds by plants is inducible by herbivory or pathogen attack (Zengerl and Berenbaum 1997; Zengerl et al. 1997; Siemens and Mitchell-Olds 1998). Similarly, defense mechanisms employed by insects can be induced by parasites (Kraaijeveld and Godfray 1999). Finally, courtship effort by animals may be influenced by the attractiveness of their mates (Sheldon 2000). Because genotypes are likely to differ in the magnitude of their responses to such cues, their response will add to the variation in allocation at a particular level of the hierarchy. These processes seem unlikely to alter the basic conclusions of our model, but their influence may increase overall variation in allocation and cause levels of variation within hierarchies to differ among populations.

APPENDIX

Table A1: **G** matrices for three variance ratios ($V_{P_1} : V_{P_2}$) and three patterns of resource allocation to T_1, T_3, and T_4

Variance ratio ($V_{P_1} : V_{P_2}$)	$T_1 = 6, T_3 = 1.2, T_4 = 2.8$[a]			$T_1 = 6, T_3 = 3, T_4 = 1$[b]			$T_1 = 1.8, T_3 = 6, T_4 = 2.2$[c]		
	T_1	T_3	T_4	T_1	T_3	T_4	T_1	T_3	T_4
.1 (.0003 : .003):									
T_1	.03	−.009	−.021	.03	−.023	−.008	.03	−.022	−.008
T_3		.051	.042		.065	−.043		.218	−.196
T_4			.063			.050			.204
1 (.0003 : .0003):									
T_1	.030	−.009	−.021	.030	−.023	−.008	.030	−.022	−.008
T_3		.008	.002		.022	.001		.036	−.014
T_4			.020			.007			.022
10 (.003 : .0003):									
T_1	.300	−.090	−.210	.300	−.225	−.075	.300	−.220	−.081
T_3		.032	.058		.174	.051		.181	.039
T_4			.152			.024			.042

Note: The variance ratios are those compared in figures 2 and 3. Numbers on the diagonals are genetic variances, and those on the off-diagonals are genetic covariances.

[a] Allocation patterns correspond to starting allocation 1 in figures 2 and 3.

[b] Allocation patterns correspond to the final allocations in figure 2*c*.

[c] Allocation patterns correspond to the final allocations in figure 2*d*.

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