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# THE QUARTERLY REVIEW of BIOLOGY



## THE FITNESS OF FITNESS CONCEPTS AND THE DESCRIPTION OF NATURAL SELECTION

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### ABSTRACT

*"Fitness" has been used to indicate a measure of general adaptedness, and to indicate a short-term measure of reproductive success. The former concept seems unproductive in evolutionary biology, but consensus on the exact form of the latter might be possible. Fitness as a short-term measure of reproductive success can be defined from the demographic recurrence equations for genotypic number; it refers to a genotype or to a genotypic combination, if genotypes interact. Fitness summarizes a model for genotypic demography for a given set of assumptions about the population and the genotypic and individual interactions within it. For a population growing at a constant rate, demographic genotypic fitness has the same shape as reproductive value at birth; but reproductive value refers to a cohort of a genotype, while demographic genotypic fitness refers to organisms of one genotype at one moment in time. This is a major conceptual difference, although the numerical identity between demographic genotypic fitness and reproductive value for a population growing at a constant rate explains why models of life history evolution based upon reproductive value are successful.*

*The Secondary Theorem of Natural Selection (Robertson, 1968) predicts the selection response in mean trait value by the genetic covariance between trait and fitness. Selection on a quantitative trait is often formulated as involving the heritability and the phenotypic covariance between trait and fitness or the phenotypic selection gradient  $\beta$ , the (partial) regression of fitness on the trait. The change in the covariance between the genotypic and the phenotypic level introduces an assumption on the additivity of fitness. The selection gradient, as a regression, focuses on differences in fitness as derived from differences in the trait. In the Secondary Theorem, trait and fitness play equivalent roles. The Secondary Theorem implies a different understanding of the process of selection from a phenotypic selection gradient and a heritability, on those two counts. Fitness might arise from the phenotype in interaction with the environment, but phenotype and fitness might both arise as consequences of development. The study of selection thus becomes the study of the biological mechanisms underlying and generating the genetic covariance between phenotype and fitness.*

### INTRODUCTION

THE MOST SUCCINCT as well as the most amusing description of fitness was given by Stearns (1976): "Fitness: something

everyone understands but no one can define precisely." Since that time, some progress has been made toward clarifying what it is we don't understand and toward defining fitness precisely. We might feel near to a consensus

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(Partridge and Harvey, 1988)—that the rate of increase of a population of one genotype can, given the life history parameters of that genotype, be used as the fitness of that genotype (Charlesworth, 1980). Yet, we might be nearer to a reasoned doubt that a universally applicable definition for fitness exists, even if we do not accept all the possibilities for fitness cited by Stearns (1986) and Endler (1986), but restrict ourselves to “short-term measures of abundance.”

Textbooks, monographs and articles show a wealth of diversity in fitness definitions. Even textbooks do not totally agree, but range from: “differences in viability and fecundity are called fitness differences” to “the contribution to the next generation.” All textbooks, however, are quite clear about the *use* of fitness: Fitnesses are used as weights on the genotype frequency in the computation of the allele frequency in the next generation. The textbook version of fitness is numerical and relates to a genotype. In monographs, the diversity is higher. Charlesworth (1980) explains how to derive a single quantity representing genotypic fitness from fitness components. Sober (1984), coming from another field, tends to regard fitness as that design feature of a trait that leads to differences in survival and reproduction. Williams (1992) regards conformity to design specifications as evidence of adaptation; for him, fitness does not measure any design feature, but refers to some numerical contribution to the next generation, presumably reproductive success. Sober’s fitness seems to represent Williams’s adaptation. Williams (1992) regards selection on individuals of a genotype as the primary mechanism of selection at the genic level—that is, of selection on the information carried by the genes. Comparing the books raises the question of whether fitness “belongs to” a gene, a genotype, an individual, or a phenotypic trait. In articles there is even more diversity [apart from confusing usages, such as “parental fitness” and “offspring fitness” (Smith and Fretwell, 1974), where “recruitment” and “viability to independence from the parents” seem to be meant]. Several classifications of fitness concepts are given, but the classifications themselves differ too. Stearns (1986) and Endler (1986) use the same type of classification, but differ in the fitness measures men-

tioned. Henle (1991) contrasted the use of fitness as a description of natural selection with several ways of using fitness as a parameter of evolutionary models. Byerly and Michod (1991) tried to sort out the different contrasts used in fitness discussions, pointing out that several debates have been going on at the same time in almost identical terminology, though the actual debating points differed.

The main difference among fitness concepts is the contrast between a fitness concept that refers to the functioning of an organism (or genotype or trait), and a fitness concept that constitutes a technical term in population biology summarizing numerical processes. The former fitness concept still retains much of the meaning that the word fitness had in common English. In this sense, fitness itself would be a cause of natural selection. In the latter usage, a new technical quantity got labeled with an existing word, instead of a new one without a priori connotations, like *geschiktheid*, Malthusian parameter, or genotypic weight. This fundamental distinction is made explicit in the paper by Byerly and Michod (1991) and is made implicitly by Endler (1986), who emphasizes that fitness is a description of natural selection, not an explanation, thus favoring a numerical fitness concept and rejecting any use of fitness that refers to an innate quality or a good design.

Here, we’ll be concerned only with the latter fitness concept, the technical term in population biology that summarizes numerical processes with regard to selection. Even within this restriction, many quantities are proposed as fitness measures. (See the Explanation of Symbols, p. 5.) The following three are fairly widely used (Kozlowski, 1993):

- (1) The intrinsic rate of increase,  $r$ , of a population of a single genotype growing at a constant rate is often used in life history models as the fitness of that genotype in a population of many genotypes (Charlesworth, 1980; Lande, 1982a,b; Partridge and Harvey, 1988; Charlesworth, 1992; Kawecki and Stearns, 1993).
- (2) In a population at stable numbers, the net reproductive rate  $R_0$ , the expectation at birth of lifetime reproductive success, is often used too (Charlesworth, 1980; Charnov, 1986, 1989; Grafen, 1988).

## EXPLANATION OF SYMBOLS

$\alpha$	average effect of a gene substitution
$A$	denominator of fitness measure
$\beta$	selection gradient
$B$	genotypic contribution to the gamete pool, in numerator of fitness measure
$\Delta \bar{g}$	change in mean genotypic value, generation $t - 1$ to $t$
$\Delta \bar{z}$	change in mean phenotypic value, generation $t - 1$ to $t$
$e_w$	environmental value of fitness
$e_z$	environmental value of trait
$F_{ykt}$	fecundity of a pair of a female with genotype $A_i A_j$ and a male with genotype $A_k A_l$
$g$	genotypic value of the trait
$h^2$	heritability = $V_A/V_P$ , ratio of genetic variance to phenotypic variance
$\lambda$	growth rate of the population
$l_{y,x}$	probability of survival of an individual of genotype $A_i A_j$ from age 0 to age $x$
$m$	Malthusian parameter
$m_{y,x}$	number of gametes produced by an individual of genotype $A_i A_j$ of age $x$
$m_{kl}$	mating frequency of a male with genotype $A_k A_l$
$n_{y,x,t}$	number of individuals of genotype $A_i A_j$ of age $x$ at time $t$
$N_{y,t}$	number of adults of genotype $A_i A_j$ at time $t$ : $N_{y,t} = \sum_{x \geq 1} n_{y,x,t}$
$p(g)$	distribution of additive genotypic values of the trait $z$
$p(z)$	distribution of phenotypic values of the trait $z$
$p_{y,x-1}$	probability of survival of an individual of genotype $A_i A_j$ from age $x - 1$ to age $x$
$p_t$	allele frequency of allele $A_1$ in newly born individuals at time $t$
$q_t = 1 - p_t$	allele frequency of allele $A_2$ in newly born individuals at time $t$
$r$	intrinsic rate of increase of a population
$R$	selection differential for genotypes
$R_0$	net reproductive rate
$s$	selection differential for individuals
$s_y$	probability of survival of an individual of genotype $A_i A_j$ from age $x$ to age $x + 1$
$v_y$	probability of survival of an individual of genotype $A_i A_j$ from age 0 to age 1
$v_x$	reproductive value at age $x$
$w_{y,t}$	demographic genotypic fitness of genotype $A_i A_j$ at time $t$
$w(g)$	fitness as function of genotypic value
$w(z)$	fitness as function of phenotypic value
$x$	age; $x = 0$ is age at birth
$x_{y,t}$	genotype frequency of genotype $A_i A_j$ at time $t$
$z$	phenotypic, individual value of the trait

(3) Reproductive value at birth  $v_0$  in a population growing at a constant rate  $r$  differs from expected lifetime offspring production by the discount factor  $e^{-rx}$  for offspring born to a mother of age  $x$ . Reproductive value too is often taken to represent fitness (Schaffer, 1979; Emlen, 1984; Caswell, 1989).

These three fitness measures have in common that they are composed of fitness components: the age-dependent survival probabilities and age-dependent fecundities. The fitness components present, therefore, a common ground between models to start a derivation of fitness measures, discuss their properties, and clarify the concept fitness.

These three measures mentioned all refer to a genotype: They are based upon the growth rate of a population of a single genotype or on the expected number of offspring for a cohort of a genotype. The measures are not individual fitness measures, but measures of genotypic fitness. Quite often, however, individual survival or fecundity is measured in fitness studies in natural populations, and used as fitness associated with a given trait value. Field studies often use an individual fitness concept, while theoretical studies usually rely on a genotypic fitness concept. We'll try to examine this difference, and show how it affects our appreciation of natural selection.

#### THE CAUSES AND CONSEQUENCES OF NATURAL SELECTION

If fitness is not itself the cause of natural selection, what then are the causes of fitness differences? This is one of the two "important and interesting questions" in the study of natural selection (Endler, 1986: 33): the first being the biological reasons for fitness differences, and the second being the evolutionary dynamics, given the differences in fitness components. Stearns (1986) refers to the study of the causes and consequences of fitness differences. Both Stearns (1986) and Endler (1986) seek a functional explanation for any differences in fitness components. Endler and McLellan (1988) and Scharloo (1984) see such a functional explanation as a major task of population genetics. The causes of fitness differences have to be sought both in the biology of fitness components and in the demographic shaping of fitness components into fitness. The consequences of fitness differences are changes in trait values, optimization of traits, and the patterns of co-occurrence of traits.

The causes of fitness differences might be difficult to assess, but a first strategy is to describe the association between a trait considered to be of interest and fitness, or, more usually, a fitness component. Such a relation between the value of a trait and the value of fitness is called a fitness function (Lande, 1979; Anholt, 1991) or a fitness profile (Robertson, 1955; Falconer, 1981). A fitness function or fitness profile refers to all trait values possible. For a restricted range of trait values, a linear approximation of the fitness function —

the selection gradient — is often used. Fitness profiles "represent an observed relationship, but one should be very cautious in inferring any causal relationship" (Robertson, 1955). A fitness profile can arise in two ways (Robertson, 1955, 1956; Falconer, 1981), as has been emphasized for stabilizing selection: Fitness might be "assigned" to a trait on the basis of the phenotypic value, or both fitness and trait might arise from the same set of genes (Fig. 1).

If individuals are selected strictly on the basis of a finished phenotype, the relation between trait value and fitness arises from the selection procedure itself. The selection procedure will be given by some constraint or problem in the environment, and, as in artificial selection, will use individual phenotypic values. In this sense fitness arises from the interaction of phenotype and environment, independent of the genotype, and trait value differences cause fitness differences. This view prevails strongly in field studies or field-related studies of natural selection. The statement, "Because natural selection acts on phenotypes and is blind to the underlying genotype . . ." (Anholt, 1991), aptly expresses this view. It is the view that "the fitness of an individual is the result of the interaction of the phenotype with the environment, and not an intrinsic feature of either" (Wade and Kalisz, 1990). In this view, to study natural selection is to investigate how fitness depends upon phenotype; that can be experimentally approached, for instance, as in the study by Anholt (1991), by manipulating the environment to create a greater range of phenotypes, or, as advocated by Wade and Kalisz (1990), by manipulating the environment to create different fitness functions for the same trait in different environments.

But the relation between trait and fitness might be developmental and incidental, in that trait differences accompany fitness differences, but do not give rise to fitness differences. Many quantitative traits might be related to fitness, without being themselves a focus of selection. A recent example of such a relation might be found in the cowpea weevil *Callosobruchus maculatus*. In the experiments of Møller et al. (1989), development rate, female adult weight, and female fecundity are genetically correlated. Sibly et al. (1991) show that two fitness com-

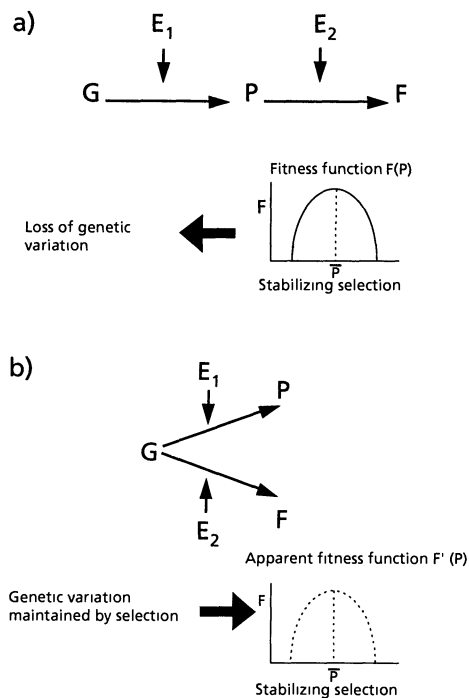


FIG. 1. A DIAGRAM OF TWO FUNDAMENTALLY DIFFERENT VIEWS OF THE RELATION BETWEEN GENOTYPE, PHENOTYPE, AND FITNESS (ROBERTSON, 1956; FALCONER, 1981, CHAPTER 20)

$G$  represents the genotype,  $P$  the phenotype,  $F$  the fitness,  $E_1$  the environmental influences between genotype and phenotype,  $E_2$  the environmental influences between genotype or phenotype and fitness ( $E_1$  and  $E_2$  might be identical),  $F(P)$  the stabilizing selection function (fitness as function of the phenotypic value), and  $F'(P)$  the apparent stabilizing selection function, mean fitness value associated with a phenotypic value. (a) Genotype and environment determine the phenotype of an individual. Natural selection acts on the phenotypic value; phenotype and environment determine fitness. The case where the mean phenotypic value has highest fitness is illustrated; phenotypic deviation from the mean leads to increasingly lower fitness. This type of stabilizing selection leads to loss of genetic variation (Wright, 1935; Robertson, 1956; Nagylaki, 1989b). (b) Genotype and environment determine fitness, and, independently, genotype and environment determine the phenotype for a selectively neutral trait. Assume that the fitnesses are such as to maintain genetic variation. Under this premise, the genetic association between phenotype and fitness leads to an apparent stabilizing selection function  $F'(P)$  (Robertson, 1956; Barton, 1990; Gavrillets and de Jong, 1993).

ponents are linearly related to adult weight — development rate decreasing with female weight and fecundity increasing with female weight—and that total fitness is highest at an intermediate optimum weight. Yet, adult weight differences are unlikely to cause differences in development rate to adult, and development rate differences rather than weight differences are the cause of fecundity differences. The phenotype “weight” develops together with the fitness components. The association between the phenotypic trait weight and the fitness components development rate and fecundity arises from shared physiological processes during larval growth. Selection on weight seems an incidental consequence of genotypic fitness differences for development rate.

Falconer (1981) (Chapter 20) extensively discusses the associations between trait and fitness on the basis of the ideas of Robertson (1955, 1956). Robertson (1955) discussed the association between the form of the fitness profile and the relation of the trait to fitness. Robertson (1956) contrasted a model of stabilizing selection on phenotypic trait value with a model of apparent stabilizing selection owing to the maintenance of genetic variation (Fig. 1). The field biologists’ view of stabilizing selection, premised upon selection against the deviation from the phenotypic mean, has the loss of genetic variation as a consequence (Wright, 1935; Robertson, 1956; Nagylaki, 1989b). The geneticists’ view of fitness owing to properties of the genotypes has the maintenance of genetic variation by the genotypic fitnesses as premise, and apparent stabilizing selection on an associated nonselected phenotypic trait as a consequence (Robertson, 1956). Barton (1990), extending Robertson’s model, showed that genetic variation maintained by a mutation-selection balance, as well as by overdominance, leads to apparent stabilizing selection on an additive pleiotropic nonselected trait. Gavrillets and de Jong (1993), again extending Robertson’s (1956) idea, showed that epistatic interactions in fitness are a much more potent cause of apparent strong stabilizing selection on an associated additive pleiotropic nonselected trait than overdominance. The higher the epistasis in determining fitness values, the stronger would be the clustering of

TABLE 1  
The four selection gradients

Type of selection gradient		Notation	Definition	Reference
Genotypic	Individual	$\beta_{wg}$	$\text{cov}\{g, w(g)\} / \text{var}\{g\}, dw(g)/dg$	(1), (3)
Phenotypic	Individual	$\beta_{wz}$	$\text{cov}\{z, w(z)\} / \text{var}\{z\}, dw(z)/dz$	(1), (2), (3)
Genotypic	Mean values	$\beta_{mw,mg}$	$\overline{dw(g)/dg}, \Sigma_{loci} 2p_i q_i \alpha_{w,i} \alpha_{z,i} / \Sigma_{loci} 2p_i q_i \alpha_{z,i}^2, \text{cov}_A(w, z) / V_A(z)$	(1), (4)
Phenotypic	Mean values	$\beta_{mw,mz}$	$\overline{dw(z)/dz}, \text{cov}_F(w, z) / V_F(z)$	(1)

Note: (1) Lande, 1979; (2) Lande and Arnold, 1983; (3) Iwasa et al., 1991; (4) Robertson, 1968.

individual fitness values around the apparent fitness function (cf. Fig. 4b in Gavrilov and de Jong, 1993), giving the clear impression of selection on the phenotype itself.

The two views of the relation between phenotype and fitness differ fundamentally. We must see whether the two views are reflected in our descriptions of natural selection, or whether any description of natural selection forces us to accept one or the other view of the relation between trait and fitness. Before doing that, we need to have our concepts and tools in place. We need to know what we mean by fitness, and how to handle the fitness functions.

#### THE CAUSES OF NATURAL SELECTION

##### *The Biology of Differences in Fitness Components*

The study of the causes of fitness differences is the study of the biology underlying differences in fitness components. Even if the definition of fitness might be unclear, it is quite clear what the components of fitness should be: viability, fecundity, and mating success, to name a few. A great part of evolutionary biology is concerned with differences in fitness components. In experiments and field studies, one of two procedures is followed: to choose a trait and investigate the association between trait values and fitness values, or to choose a genotype, and investigate the association between a genotype and fitness values.

The difference between the two procedures seems practical, not fundamental: A trait value is used when genotypes are not recognizable for individuals, as for a quantitative character, and genotypes are used whenever one-locus genotypes can be discerned, as in many color polymorphisms and electrophoretic polymorphisms. Both procedures estimate a selection

gradient. The general procedure for showing selection on quantitative traits was discussed by Wade and Kalisz (1990). Individuals differing in the trait are put in a graded series of relevant environments. A fitness component of interest that can be measured for individuals is chosen. The regression coefficient  $\beta_{wz}$  of fitness component  $w$  on phenotypic trait value  $z$  indicates the selection gradient within any environment (Lande and Arnold, 1983; Arnold and Wade, 1984) (Table 1). Both a regression coefficient  $\beta_{wz}$  differing from zero and a change in  $\beta_{wz}$  with the environment are evidence for selection on the quantitative trait. At first sight, the selection gradient approach for quantitative traits has little in common with the approach for establishing the presence of selection on one-locus genotypes. If one shifts attention from the electrophoretic difference used to recognize the genotypes to the traits the genotypes represent, the basic similarity can be seen most easily in the functional approach for detecting selection between allozyme variants (de Jong et al., 1972; Clarke, 1975; de Jong and Scharloo, 1976). The trait of importance is enzyme activity: Since the allozyme genotypes differ in enzyme activity, the genotypic value for enzyme activity and the genotypic value for the fitness component can be used. The regression  $\beta_{wg}$  of the genotypic value of fitness on the genotypic value of the trait represents the selection gradient. In both cases, for quantitative traits and for recognizable genotypes, a selection gradient  $\beta$  is used to represent the selection on the trait. Wade and Kalisz (1990) and Clarke (1975) present the same approach to the recognition of the presence of selection. Both Clarke (1975) and Wade and Kalisz (1990) advocate using a range of environments to investigate the dependence of the selection gradient  $\beta$  on the

environment in order to investigate the causation of fitness differences. The difference between Wade and Kalisz (1990) and Clarke (1975) is whether the selection gradient is the regression coefficient of individual fitness on individual trait value,  $\beta_{wz}$ , or the regression coefficient of genotypic fitness value on genotypic trait value,  $\beta_{wg}$ . The difference between the two procedures is not that one deals with quantitative traits and the other with polymorphic loci, but that the one estimates a selection gradient  $\beta_{wz}$  based on individual values, and the other estimates a selection gradient  $\beta_{wg}$  based on genotypic values.

#### *From Fitness Components to Fitness*

In this section, we'll investigate whether a summary individual fitness or genotypic fitness can be derived from the fitness components, assuming that a genotype has pleiotropic effects on all fitness components. Such a summary fitness should account for the changes in the *numbers* of a genotype born in successive time units. The most widely accepted fitness definition (see Partridge and Harvey, 1988) has this demographic basis (Charlesworth, 1980). We'll use the demographic expressions to examine fitness definitions. On the basis of the demography of genotypes, fitness turns out to refer to the genotypic contribution at any one instant of time to the next cohort born, *not* to an individual's contribution over the individual's lifetime to all the cohorts born in that period. That is, a summary fitness will turn out to refer to a genotype; in demography, fitness would be considered a "vertical" relationship. In contrast, reproductive value at birth proves to refer to a cohort; in demography, reproductive value would be considered a "horizontal" relationship. Fitness and reproductive value at birth have formulations that look very similar and are similarly composed from the fitness components, but conceptually they are quite different.

#### No Interactions between Individuals

One point of general importance about fitness is that it should refer to an independent unit (Christiansen, 1984; Grafen, 1988). This

excludes from consideration any allelic fitness in diploids, as used by Sibly (1989), and implies that care has to be taken if the population reproduces sexually (Christiansen, 1984; Keller, 1987). The simplest situation in sexual diploids involves independent survival of each individual from zygote formation to death, random mating between gametes at discrete points in time, and homogeneity of interactions within the population.

In the following, it will be supposed that one locus pleiotropically affects all fitness components, following Charlesworth (1980). For polygenic determination of fitness components, Lande (1982a,b) showed that a fitness definition similar to Charlesworth's (1980) is valid. In a multivariate treatment of selection on fitness components, the genetic variance-covariance matrix relating the fitness components is due to pleiotropy. The degree of pleiotropy between the several fitness components might differ and does not have to be total, as in a one-locus model. Since the fitness expression arrived at does not depend upon the number of loci or degree of pleiotropy, the argument will be set out for one locus with pleiotropic effects on all fitness components.

At the basis of all discussion of fitness lie the demographic recurrence equations for genotypic numbers. These demographic recurrence equations contain both the change in total number and the change in genotype frequency; they determine both the dynamics of the population and the course of natural selection. The units of these equations could be the number of newly born of each genotype because the newly born are the earliest stage of independence in the simplest life history. In general, the demographic recurrence equations for genotypic numbers are assumed to apply beginning at the earliest life history stage that lives independently of other individuals. At time  $t$ , the numbers of newly born of each genotype at a locus with two alleles  $A_1$  and  $A_2$ , with random mating between gametes independent of the age of the parents, and with equal viabilities and gamete production in males and females leading to equal male and female fitnesses, become (see the Explanation of Symbols for notation, and Appendix 1 for more detail):



TABLE 2  
Derivation of fitness measures from genotypic contribution of gamete pool

Numerator fitness	Denominator fitness	Fitness	Reference
$x_{kl,t} \sigma n_{y,x,t} \varphi m_{y,x}$	$n_{y,x,t} \varphi$	$x_{kl,t} \sigma m_{y,x}$	Gregorius, 1984 <sup>1</sup>
$\frac{1}{2} p m_{12,x,t} \varphi m_{12,x}$	$n_{12,x,t} \varphi$	$\frac{1}{2} p m_{12,x}$	Taylor, 1990 <sup>2</sup>
$\frac{1}{2} p m_{12,x} \sigma m_{12,x} \phi_{11,0} + n_{12,x} \phi_{12,x}$	$n_{12,x,t}$	$\frac{1}{2} p m_{12,x} \phi_{11,0} + \phi_{12,x}$	Taylor, 1990 <sup>2</sup>
$\sum_{x \geq 1} n_{y,x} m_{y,x}$	$\sum_{x \geq 1} n_{y,x,t-1}$	$\sum_{x \geq 1} n_{y,x} m_{y,x} / \sum_{x \geq 1} n_{y,x,t-1}$	Kimura, 1958
$\sum_{x \geq 1} n_{y,x} m_{y,x}$	$\sum_{x \geq 1} n_{y,x,t}$	$\sum_{x \geq 1} n_{y,x} \sigma m_{y,x} / \sum_{x \geq 1} n_{y,x,t}$	Charlesworth, 1970; Gregorius, 1984
$\sum_{x \geq 1} n_{y,x} m_{y,x}$	$n_{y,0,t-1}$	$\sum_{x \geq 1} n_{y,x} m_{y,x} / n_{y,0,t-1}$	Charlesworth, 1980
$n_{y,0,t}$	$n_{y,0,t-1}$	$n_{y,0,t} / n_{y,0,t-1}$	Murray, 1990

Note: <sup>1</sup> Fitness is given as pertaining to a genotype  $A_i A_j$  female of age  $x$  with offspring from  $A_k A_l$  male.

<sup>2</sup> Fitness is given as pertaining to a genotype  $A_1 A_2$  female of age  $x$  with  $A_1 A_1$  offspring.

$$\begin{aligned}
 n_{11,0,t} &= p_t (\sum_{x \geq 1} n_{11,x-1,t-1} \varphi \phi_{11,x-1} m_{11,x} \\
 &\quad + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1} \varphi \phi_{12,x-1} m_{12,x}), \\
 n_{12,0,t} &= q_t (\sum_{x \geq 1} n_{11,x-1,t-1} \varphi \phi_{11,x-1} m_{11,x} \\
 &\quad + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1} \varphi \phi_{12,x-1} m_{12,x}) \quad (1) \\
 &\quad + p_t (\sum_{x \geq 1} n_{22,x-1,t-1} \varphi \phi_{22,x-1} m_{22,x} \\
 &\quad + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1} \varphi \phi_{12,x-1} m_{12,x}), \\
 n_{22,0,t} &= q_t (\sum_{x \geq 1} n_{22,x-1,t-1} \varphi \phi_{22,x-1} m_{22,x} \\
 &\quad + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1} \varphi \phi_{12,x-1} m_{12,x}).
 \end{aligned}$$

A summation represents the contribution of females of a given genotype alive at time  $t - 1$  to the gamete pool at time  $t$ . The summation is over all ages of adults ( $x \geq 1$ ) that are reproducing at time  $t$ .

Many fitness definitions are possible in keeping with these numbers of newly born. All fitness measures are aimed at a per capita quantity: but the demographic recurrence equations for genotypic numbers are not in a per capita form. To obtain a per capita quantity, all fitness definitions use a mathematical trick: that  $(B/A) * A = B$ . We can take the contribution by a genotype or class to the gamete pool, divide it by the number in some class of organisms to find a fitness measure for that class, multiply this fitness measure by the same number, and recover the demographic recurrence equations. A collection of proposals for such  $B$ ,  $A$ , and  $B/A$  is given in Table 2; their wider derivation is given in Appendix 1.

Two classes of fitness measures are discernible in Table 2: fitness measures that center on females of a particular age and genotype, and fitness measures that only focus on females of a particular genotype (male fitness can be defined in exactly the same way). Measures of the fitness of a female of a given ge-

notype and age were proposed by Gregorius (1984) and Taylor (1990). Gregorius (1984) defined the fractional fitness  $W'_{ij,x,kl}$  of a female of age  $x$  with genotype  $A_i A_j$  as the number of her successful gametes from fertilizations by  $A_k A_l$  males (Table 2). Gregorius's definition of fractional fitness involves the genotype frequencies in males. Taylor (1990) defined a series of fitness measures for classes of organisms. The simplest would be the fitness  $W_{ij,x,ik}$  of females of age  $x$  with genotype  $A_i A_j$ , giving rise to newborn of genotype  $A_i A_k$  (Table 2, second line). Taylor's definition involves the gene frequencies in males, and the genetic similarity ( $\frac{1}{2}$  or 1) between mother and offspring. Instead of counting newborn, one might count adults just before reproduction; Taylor's definition can then be modified (Table 2, third line).

The fitness expressions by Gregorius (1984) and Taylor (1990) are easily confused with individual fitness for a certain class of females: The division of the contribution by that class of females to the newly born by the number of females in that class is possible (Table 2). Yet, it has to be remembered that such an "individual" fitness is defined for a class of identical females. Individual phenotypic deviation is not taken into account. Moreover, the fitness measure is actually defined for a genotypic combination, of mother and offspring, or of male and female.

Fitness measures that focus only on a particular genotype have also been proposed. All these fitness measures are concerned with the total contribution to the gamete pool by females of all ages and the genotype of interest

(Table 2). To arrive at a fitness measure, this total contribution by the genotype to the gamete pool is divided by either the number of adults of that genotype in the previous time unit (Kimura, 1958, Table 2, line 4), the number of adults of that genotype in the present time unit (Charlesworth, 1970; Gregorius, 1984, Table 2, line 5), or by the number of newborn of that genotype in the previous time unit (Charlesworth, 1980, Table 2, line 6). The standard definition of demographic genotypic fitness is the last one mentioned: the total contribution by a genotype to the gamete pool, divided by the number of newborn of the same genotype one time unit earlier. This division is not a very obvious choice, as the newborn of the same genotype one time unit earlier are clearly not producing all of the contribution of the genotype to the newborn in the present time unit. Dividing by the number of newborn of the same genotype one time unit earlier is, however, in keeping with accounting the recurrence equations in the number of newborn, and is therefore the consistent and preferred formulation for fitness. For this demographic genotypic fitness, with random mating of gametes and equal fitness of males and females, the classical selection formulas with genotypic weights are recovered. Moreover, as in the classical selection formulas, the recurrence equations are kept in zygotes (Prout, 1965).

Demographic genotypic fitness is a contribution to the newly born by organisms of all ages of one genotype, scaled to the number of newly born of that genotype in the previous time unit. Unless the growth rate of the population and the genotype frequencies are constant, demographic genotypic fitness is frequency and density dependent (Charlesworth, 1980). With constant genotype frequencies and a stable age distribution, the growth rate  $\lambda$  of the population is constant. Changes in the age distribution and growth rate bring changes in allele frequency among the newly born, even if fitness components are such that there would be no allele frequency change in stable age distribution (Charlesworth, 1980). Stable age distribution applies to stable polymorphism and approximately when selection is weak. The division in the definition of demographic genotypic fitness can be done in the case of

a constant growth rate of the population and constant genotype frequencies. Demographic genotypic fitness  $w_y$  becomes, independent of time,

$$w_y = \sum_{x \geq 1} \lambda^{-x+1} l_{y,x} m_{y,x}. \quad (2)$$

Although demographic genotypic fitness  $w_y$  is now independent of time, the summation is still done at time  $t$ , over all ages of the adults that are present. This has to be contrasted with other fitness measures. With constant density,  $\lambda = 1$  and

$$w_y = \sum_{x \geq 1} l_{y,x} m_{y,x}. \quad (3)$$

At constant density, the demographic genotypic fitness numerically equals the total number of successful gametes an average individual produces during its whole life span, the expected value for the per individual gametic fitness of Gregorius (1984). For a population mating randomly at the level of the gametes, this is equivalent to the total number of zygotes produced by an average individual during its whole life span, the expected value for the per individual zygotic fitness of Gregorius (1984). Under random mating of gametes, expected "zygotic fitness" is numerically equal to expected lifetime reproductive success for a genotype (Grafen, 1985, 1988). Expected lifetime reproductive success for a genotypic cohort gives the net reproductive rate  $R_{0,ij}$  for that genotype (Charnov, 1986, 1989). It remains true, however, that in the expected values of gametic fitness and zygotic fitness (Gregorius, 1984), and in the expected value of lifetime reproductive success (Grafen, 1988), the summation is for a cohort over the ages the individuals of the cohort reach. Gametic fitness, zygotic fitness, and lifetime reproductive success can therefore be held to refer to an average individual for its cohort, and to represent the average individual's contribution to the next generation, from birth to death. In contrast, the summation in demographic genotypic fitness is at one point in time over individuals of all ages, born at different times. Even when demographic genotypic fitness on the one hand, and expected lifetime reproductive success, expected zygotic fitness, and expected gametic fitness on the other hand, are numerically the same, there is a huge conceptual difference. The difference—between sum-

mation over the ages one cohort reaches in lifetime reproductive success and over the ages of individuals from different cohorts present at the same time in demographic genotypic fitness — has as a consequence that lifetime reproductive success is not generally predictive of fitness, but only under constant density. One might try to save an individual fitness concept related to expected lifetime reproductive success for a population with a constant growth rate rather than constant number ( $\lambda \neq 1$ ), by stating that offspring produced further in the future should be discounted by a factor that depends on the growth rate of the population [for instance, this is the way Grafen (1988) represents Charlesworth's (1980) fitness definition; see also Reeve and Sherman, 1993]. Such a fitness definition equates fitness with reproductive value at birth: another quantity that refers to a (genotypic) cohort (Fisher, 1930). The discounting gives the right formula for fitness, but at the price of having to grasp why individual fitness should display such a discount — something that is not immediately obvious. In demographic genotypic fitness, the different age classes are present in proportions that depend upon the population growth rate, and it is therefore obvious that the population growth rate influences demographic genotypic fitness.

Following Fisher's (1930) description of the Malthusian parameter, Charlesworth (1980) proposes using the stable age distribution growth rate  $\lambda_y$  of a population of one genotype  $A_i A_j$  with the same  $l_{y,x}$  and  $m_{y,x}$  schedule to estimate fitness  $w_y$  in a population with a number of genotypes. This growth rate  $\lambda_y$  has the same properties as  $w_y$ , but it is an indirect measure of fitness. It is often used, however, in the form  $r_y = \ln(\lambda_y)$  (Partridge and Harvey, 1988; Kozłowski, 1993), and perhaps it is the most widely used fitness measure in life history theory.

The substitution of the stable age distribution growth rate  $\lambda_y$  of a population of one genotype for fitness  $w_y$  in a population of three genotypes invites confusion between fitness  $w_y$  and the growth rate of a genotype within a population of three genotypes,  $\lambda_y = n_{y,0,t} / n_{y,0,t-1}$  (Table 2, line 7). The consensus is that the latter quantity is not a correct description for natural selection (Deniston, 1978; Charles-

worth, 1980; Emlen, 1984; Keller, 1987; Maynard Smith, 1991), though one can still find it as either an a priori definition of fitness (Byerly and Michod, 1991), or cited as a preferable description of genotypic dynamics (Murray, 1990). This fitness definition can only be used for asexuals (de Jong, 1990). In the original derivation of the Fundamental Theorem of Natural Selection, Fisher implicitly referred to asexuals; this follows from the description of the group the Malthusian parameter refers to, and from the form given for the additive genetic variance (Fisher, 1930).

Selection maximizes mean demographic genotypic fitness. For density-dependent juvenile viability, this directly implies that for weak selection and a stable age distribution, selection maximizes the equilibrium density of the newly born (Roughgarden, 1976; Charlesworth, 1980). Maximizing reproductive value, at any age, implies maximizing part of the fitness expression, and therefore maximizing reproductive value at a certain age can in some cases be used for maximizing fitness (Schaffer, 1979; de Jong and van Noordwijk, 1992). Demographic genotypic fitness, and — at a stable age distribution — growth rate of a population made up of that genotype, reproductive value at birth, and carrying capacity are four guises of the same fitness criterion, not different ones as considered by Henle (1991). This leads to versatility in use. It has to be remembered that these fitness measures depend upon some assumptions about the life history, most importantly lack of interactions between genotypes.

#### Interactions between Individuals

Interactions between individuals disturb this idyll. When mating between individuals is random, and the combination of genotypes of male and female determines fecundity, the demographic fitnesses differ. It is no longer the individual but rather the pair that is the independent unit in reproduction (Kempthorne and Pollak, 1970). Fitness in a sexual population therefore has to refer to the genotypic combination in the pair (Christiansen, 1984; Keller, 1987). Demographic fitness has to be defined per genotype combination in the pair; this leads to a change in the relation between the growth rate of the population and fitness.

Demographic recurrence equations analogous to those above (1) for the number of newly born of each genotype can be written for random mating in each mating season (de Jong, 1982b; Abugov, 1983, 1985, 1986) (Appendix 2). Fecundity of the pair depends upon the genotypic combination in the pair. It is possible to define a demographic pair fitness and to define a male fitness up to maturity in a manner analogous to the definition of demographic genotypic fitness (see Appendix 2 for the definitions). Allele frequency change depends only upon demographic pair fitness. Demographic pair fitness and the growth rate of a population made up of that genotype are not equivalent (Abugov, 1983, 1985). The growth rate of a population of one genotype becomes  $\lambda = w_{\text{pair}}/w_{\sigma}$ , including male fitness as well as demographic pair fitness; the quotient indicates that the growth rate of a population of one genotype depends mainly upon female fitness. The growth rate of a population of one genotype cannot be used to predict demographic pair fitness and the outcome of selection. This has implications for the models of optimization of clutch size in bird studies. Even if fecundity is only dependent upon the female's genotype, the pair fitness that has to be used in predicting life history results is not equal to the growth rate of a population of one genotype. Selection does not maximize growth rate (Kempthorne and Pollak, 1970; Pollak, 1978) or equilibrium number (de Jong, 1982b; Abugov, 1985). Selection maximizes mean demographic pair fitness only if Hardy-Weinberg proportions are found in the newly born (Abugov, 1985).

Another possibility for genotypic interaction in fitness is that fitness can be defined only for a combination of parent and offspring genotypes (Templeton, 1979). If, for instance, the number of eggs in a clutch depends only on the genotype of the mother, but survival in the clutch depends on the genotype of the individual offspring in the clutch, a one-locus demographic selection model has to use seven fitnesses, one for each mother-offspring combination, apart from whatever might be happening with the males. In such a seven-fitness model, the proper age of accounting is not the newly *born*, but the newly *independent* young. The seven-fitness system reduces to the usual

three-fitness system if either fecundity or clutch survival is independent of the genotype. Without any selection in the males, and with equal survival within the nest for the offspring, the pair-offspring combinations reduce to selection in one sex; female fitness is then maximized (Cannings, 1969; Abugov, 1985).

The assumptions of random mating at the level of the gametes and equal age-specific survival and fecundity in males and females are too specific to justify the use of the growth rate  $\lambda_j$  of a population of genotype  $A_i A_j$  as the "fitness" of that genotype. Therefore, maximization of  $\lambda$  without considering the appropriateness of the underlying model cannot be used in life history theory to predict optimization of traits. Abugov (1986) suggests using a weighted mean of the fitness components per age class—the fitness components per age class thus bring us to the model of a structured population by Taylor (1990). Maximization under selection of a weighted mean was shown for the equilibrium density in an age-structured population subject to density-dependent selection in each age class (Iwasa and Teramoto, 1980).

#### Population Influences

The appearance of the population growth rate in demographic genotypic fitness shows that fitness does not only depend on individual fitness components like viability and fecundity, but acquires a component that is owing to properties at the population level. For density-dependent number regulation, this implies that density variation in space and in time influences overall fitness. Density variation in space has been treated in several models (Kisdi and Meszner, 1992). An example appears in the models of the evolution of insect clutch size and competitive coexistence. There, the variance of the distribution of egg-laying females over local juvenile food patches influences fitness (Atkinson and Shorrocks, 1981; de Jong, 1982a). Density variation in time has potentially a very large effect. Net reproductive rate  $R_0$ , expected lifetime reproductive success, and reproductive value at birth are equal to demographic genotypic fitness  $w$  at constant population size. Interest is in what would happen when population size is not constant, but on average neither increases

nor decreases. Charnov (1989) assumes that it is satisfactory to use  $R_0$  computed for  $\lambda = 1$  when actually  $\bar{\lambda} = 1$ . This involves two points, (1) that average  $R_0$  and average  $w$  are the same under fluctuations in number; and (2) that average  $w$  is the right quantity to use for predictions. Neither arithmetic nor geometric average  $R_0$  are identical to arithmetic and geometric average  $w$ , but the average of  $R_0$  over cohorts and the average of  $w$  over time units do not differ much in a population varying mildly in number. In a population showing some little stochastic variation in number, assuming  $R_0$  and fitness to be identical seems good enough for a qualitative prediction. The second point is more important. It has to be shown whether any average demographic genotypic fitness is the appropriate summary fitness measure relevant to the changes in the numbers of the genotypes in any population with major environmental variation in time or with variation due to nonlinear dynamics. Neither arithmetic nor geometric mean demographic genotypic fitness is predictive of the actual genotypic dynamics with density variation in time owing to nonlinear dynamics. For instance, in a stable two-point cycle, where population size on average neither increases or decreases, neither the geometric nor the arithmetic mean fitness is appropriate (de Jong, 1990). Density variation in time owing to nonlinear dynamics leads to different summary fitnesses for genotypes with identical fitness components (de Jong, 1990: 302, 303). Density variation in time owing to environmental variation leads to different fitness values for different degrees of environmental variation (Kisdi and Meszner, 1992, and references therein). The invadability criteria differ, but can be found according to the same rule (Metz et al., 1992).

To find fitness from fitness components means constructing a model for genotypic demography, in accordance with life history constraints, such as pair fitness, and in accordance with population characteristics, such as inhomogeneous interactions between individuals. If fitness is a technical tool used to represent some model of selection (Stearns, 1986), it is the detail of the model that is informative, rather than a summarizing quantity called fitness.

#### THE CONSEQUENCES OF NATURAL SELECTION

##### *Selection on Trait Values*

The investigation of natural selection begins with differences in fitness components, and proceeds by assessing what is the proper fitness to use for the population and selection problem addressed. Evidence for selection on a trait is compiled, in experiments and natural populations, by investigating the regression of fitness or a fitness component on trait value. This regression estimates the selection gradient, and if many trait values are used, the vector of partial regressions of the fitness component on the traits represents the selection gradient. We will be concerned with one trait and one locus, as this condition is sufficient for our present purpose of elucidating conceptual tangles. We will be concerned with the exact definition of the selection gradient: whether the selection gradient is a phenotypic or genotypic quantity, and whether the selection gradient refers to the change of fitness with trait value, or to the change of mean fitness with mean trait value (Table 1). Moreover, we will question the use of the selection gradient, a regression of fitness on trait, rather than the use of its numerator, a covariance between fitness and trait.

A selection gradient is a (partial) regression coefficient, giving fitness change owing to trait change. In using a selection gradient for describing selection, we choose therefore to introduce an asymmetry between trait and fitness. Fitness values are described as depending upon trait values. This tends to steer us toward the view that fitness is a direct function of the phenotype [Fig. 1(a)], if using the selection gradient was not already an expression of that view. In using the covariance between trait and fitness for describing selection, we choose for formal symmetry between trait and fitness. Using a covariance does not slant us toward the view that fitness arises from the phenotype, nor to the view that fitness arises from the genotype, and that the connection between fitness and trait is indirect. In a covariance, trait and fitness play an equivalent role: The origination of fitness represented in Figure 1(a) can be described by a covariance between trait and fitness, as can the origination of fitness represented in Figure 1(b).

A selection model deals with the change in

trait mean owing to differences in fitness: It might be formulated either by using a selection gradient, or by using a covariance between trait and fitness. We will show that these two selection models differ slightly in properties. Moreover, a selection model might be formulated on the phenotypic or on the genotypic level. Again, such models are not strictly equivalent, but differ in versatility and therefore in predictive power.

#### The Four Selection Gradients

The justification for estimating a selection gradient is its relation to the expected change in the mean of a phenotypic trait under selection (Lande, 1979; Lande and Arnold, 1983; Iwasa et al., 1991). Actually, the selection gradient in Lande and Arnold (1983) and the selection gradients in Iwasa et al. (1991) are not defined in exactly the same way as the selection gradient in the equation for multivariate selection in Lande (1979) (Table 1). We have already seen above that a selection gradient could refer to either an individual trait value and an individual fitness component, or to the genotypic value for the trait and the genotypic value for the fitness component. In estimating a selection gradient, most often the individual value for a fitness component is used, not the genotypic value. But fitness is found to be a property of a genotype rather than of an individual; a genotypic selection gradient should therefore be preferred (as in Queller, 1992). May the individual selection gradient be used to estimate the genotypic selection gradient? If so, under what conditions?

The influence of phenotypic selection within a generation on the individuals of a population is given by the phenotypic selection differential  $s$  (for definitions and derivations see Appendix 3). The definition of the phenotypic selection differential shows that the product of mean phenotypic fitness and the phenotypic selection differential equals the covariance between individual trait value  $z$  and individual fitness value  $w(z)$  (Jacquard, 1977; Lande and Arnold, 1983; Iwasa et al., 1991), whatever the distribution of the phenotypes and whatever the fitness values. The covariance can be written as the product of the phenotypic variance and a selection gradient, thereby

defining the individual selection gradient  $\beta_{wz}$  (Lande, 1979; Lande and Arnold, 1983; Iwasa et al., 1991). Using genotypic value for the trait and genotypic value for fitness, the product of mean genotypic fitness and genetic selection differential shows the covariance between genotypic value for the trait  $g$  and genotypic fitness  $w(g)$  (Lande, 1979; Iwasa et al., 1991). The covariance can be written as the product of the genotypic variance and a selection gradient, thereby defining the genotypic selection gradient  $\beta_{wg}$  (Iwasa et al., 1991). One selection gradient, the phenotypic selection gradient  $\beta_{wz}$ , is at the individual level, and the other selection gradient,  $\beta_{wg}$ , is at the genotypic level, or at the level of groups of individuals.

Usually, it is assumed that the phenotypic selection gradient and the genotypic selection gradient are the same; this assumption leads to the traditional  $\Delta\bar{z} = h^2s$ . However, why should the selection gradient be the same at the individual phenotypic level and at the genotypic level? It is shown in Appendix 3 that linearity of the  $w(z)$  function is the condition for the two selection gradients to be equal, and therefore the condition for  $\Delta z = h^2s$  to apply exactly rather than approximately. The genotypic selection gradient  $\beta_{wg}$  and the related genetic expression for selection (Iwasa et al., 1991) have therefore a wider applicability than the phenotypic selection gradient  $\beta_{wz}$  and its related expression for phenotypic selection within a generation (Iwasa et al., 1991) (see Table 3 for a survey of related expressions). To connect the two, some assumptions are needed. An assumption of weak selection translates easily into an assumption of linearity for the  $w(z)$  function, by way of a Taylor approximation. Iwasa et al. (1991) use the assumption of weak selection, even weak frequency-dependent selection, to justify their expression for selection (in their Appendix). Iwasa et al. (1991) point out they use a selection gradient different from the one used by Lande (1979); that is, Iwasa et al. (1991) use two selection gradients, the change of individual fitness with individual trait value and of genotypic fitness with genotypic value, neither related to the respective population means, as is the selection gradient in the equation for multivariate selection of Lande (1979). Iwasa et al. (1991)

TABLE 3  
Formulas for the change in mean under selection

Phenotypic selection differential	
$s = \text{cov}\{z, w(z)\} / \overline{w(z)}$	Lande, 1979
$s = \text{var}\{z\} \beta_{wz} / \overline{w(z)}$	Lande and Arnold, 1983
$s = \text{var}\{z\} dw/dz / \overline{w(z)}$	Iwasa et al., 1991
$s = V_P \beta_{mu, mz} / \overline{w(z)}$	Lande, 1979
Genetic selection differential	
$R = \text{cov}\{g, w(g)\} / \overline{w(g)}$	Lande, 1979
$R = \text{var}\{g\} \beta_{wg} / \overline{w(g)}$	
$R = \text{var}\{g\} dw/dg / \overline{w(g)}$	Iwasa et al., 1991
Predicted selection response	
$\Delta \bar{g} = \text{var}\{g\} \beta_{wg} / \overline{w(g)}$	Iwasa et al., 1991
$\Delta \bar{z} = h^2 \text{var}\{z\} \beta_{wz} / \overline{w(z)}$	
$\Delta \bar{z} = h^2 \text{var}\{z\} dw/dz / \overline{w(z)}$	Wade and Kalisz, 1990
$\Delta \bar{z} = h^2 \text{cov}\{z, w(z)\} / \overline{w(z)}$	Jacquard, 1977
$\Delta \bar{z} = h^2 s$	Falconer, 1981
$\Delta \bar{g} = V_A \beta_{mu, mg} / \overline{w(g)}$	Lande, 1979
$\Delta \bar{z} = h^2 \beta_{mu, mz} / \overline{w(z)}$	Lande, 1979
Observed genotypic selection response	
$\Delta \bar{g} = \Delta p \cdot d\bar{g}/dp$	Wright, 1935
$\Delta \bar{g} = \text{cov}_A(w, g) / \overline{w(g)}$	Robertson, 1968

assume the phenotypic selection gradient is equal to the genotypic selection gradient.

An alternative model for selection on a quantitative trait starts with the relation between selection response and gene frequency change and leads to a different formulation for the selection gradient, now in terms of the change of mean genotypic fitness with mean genotypic trait value (for the models see Appendix 3). The change in mean trait value between generations can be written as  $\Delta \bar{g} = \Sigma_i \Delta p_i \partial \bar{g} / \partial p_i$ , [summing over loci; this is already found in Wright (1935)]; the sum works out to be the additive genetic covariance between trait and fitness. The additive genetic covariance is therefore related to  $d\bar{w}/d\bar{g}$ , not to  $dw/dg$  (Table 1): The selection gradient  $\beta_{mu, mg} = d\bar{w}/d\bar{g}$  that can be defined on the basis of the additive genetic covariance differs from the selection gradient  $\beta_{wg} = dw/dg$  that can be defined on the basis of the genetic selection differential. This problem disappears if genotypic fitness  $w(g)$  is a linear function of the genotypic value for the trait, but otherwise a Taylor approximation of genotypic fitness around the mean genotypic value for the trait has to be used.

The phenotypic selection differential  $s$  can be related to a selection gradient  $\beta_{mu, mz}$  giving the change in mean phenotypic fitness owing to a change in mean phenotype. Lande (1979) differentiated mean phenotypic fitness toward the phenotypic trait mean; the change of the distribution with the  $z$  should again equal the phenotypic selection differential, but now as  $\text{var}\{z\} dw(z)/dz$ . Similarly, differentiating a mean genotypic fitness toward the genotypic trait mean yields the genetic selection differential  $R$ , as  $\text{var}\{g\} d\overline{w(g)}/\overline{g}$ . The assumption of the identity of  $\beta_{mu, mz}$  and  $\beta_{mu, mg}$  takes in Lande (1979) the form of the assumption that  $\nabla \ln[\overline{w(g)}] = \nabla \ln[\overline{w(z)}]$ . Again, any  $\beta_{mu, mz} \equiv dw(z)/dz$  only equals  $\beta_{wz} = dw(z)/dz$  if the fitness function  $w(z)$  is linear; otherwise, a Taylor approximation has to be used.

For a linear fitness function, all four selection gradients are equal:  $\beta_{mu, mz} = \beta_{mu, mg} = \beta_{wg} = \beta_{wz} \equiv \beta$ . For nonlinear fitness functions, assumptions of weak selection and of small per locus effects effectively lead to a first-order Taylor approximation for the fitness function. Small per locus effects and many genes lead both to a normal distribution of the trait and weak per locus selection. This implies that for a normally distributed trait, the distinctions between the selection gradients are not crucial. Lande (1979) derived his prediction equation for the vector of selection responses for any fitness function, relying upon normal distributions. Lande (1979) used all four selection gradients. In his derivation,  $\beta_{wz}$  from the definition of the phenotypic selection differential was equated to  $\beta_{mu, mz}$  from differentiating a mean phenotypic fitness toward the phenotypic trait mean;  $\beta_{wg}$  from the definition of the genetic selection differential was equated to  $\beta_{mu, mg}$  from differentiating mean genotypic fitness toward the genotypic trait mean. Lastly,  $\beta_{mu, mg}$  was equated to  $\beta_{mu, mz}$  by assumption to reach the final result (Eq. 6 in Lande, 1979). More often,  $\beta_{mu, mg}$  and  $\beta_{wz}$  are equated: as  $\beta_{mu, mg}$  is connected with the additive genetic covariance between trait and fitness, and  $\beta_{wz}$  with the phenotypic selection differential. Equating  $\beta_{mu, mg}$  and  $\beta_{wz}$  is the usual way to go from phenotypic selection within a generation to the genetic response over generations.

*The Secondary Theorem of Natural Selection*

The prediction equation for the selection response takes several different forms (Table 3). It is important to realize that the equation for the change in the trait mean can take two main forms, one form in individual trait values and individual fitness values, and one form in genotypic values for trait and genotypic values for fitness. We have to be concerned whether this has any influence upon our view of selection.

Two forms of the selection model are:

$$\Delta \bar{g} = \text{cov}\{g, w(g)\} / \overline{w(g)}, \quad (4)$$

$$\Delta \bar{z} = h^2 \text{cov}\{z, w(z)\} / \overline{w(z)}. \quad (5)$$

These are slightly but importantly different. The genotypic formulation (4) requires additivity of the trait to be exact. But in going from the genotypic form (4) to the phenotypic or individual form (5), linearity of the fitness function has to be assumed, and the formulation (5) requires additivity of both trait and fitness to be exact. Since the maintenance of any stable polymorphism requires nonadditivity in fitness, this means that the form (4) can be used to describe stable polymorphism, but not the form (5).

More important, expressions (4) and (5) represent different views of fitness and of selection. In (5), selection and transmission are separated, conceptually if not in reality. Natural selection itself is totally on the individual and phenotypic level (cf. Wade and Kalisz, 1990; Anholt, 1991). Genetic transmission only has the role of transporting part of the phenotypic selection to the next generation. In (4), selection is on the genotypic level, and cannot be separated from transmission: Phenotypic selection and transmission as one process would have to be called natural selection (cf. Endler, 1986). By equating the form (4) with the form (5), we make an important conceptual point: that natural selection always can be split into phenotypic selection and transmission. This is equivalent to stating that phenotypic fitness is sufficient for a description of selection, and that the genotype can have no separate and independent role in determining fitness or selection.

The covariance formulation of selection, as in (4) and (5), stands at the basis of a selection

gradient formulation for selection. But the covariance formulation would represent a different view of selection from the selection gradient formulation. In (4) and (5), trait and fitness play an equivalent role in the covariance: Trait value might determine fitness value, but fitness value might as well determine trait value. Changing to the selection gradient formulation implies a choice or a preference about the direction of causality, with the trait determining fitness. The trait becomes more important than fitness:

$$\begin{aligned} \Delta \bar{g} &= \text{cov}\{g, w(g)\} / \overline{w(g)} \\ &= \text{var}\{g\} \beta_{wg} / \overline{w(g)}, \end{aligned} \quad (6)$$

$$\begin{aligned} \Delta \bar{z} &= h^2 \text{cov}\{z, w(z)\} / \overline{w(z)} \\ &= h^2 \text{var}\{z\} \beta_{wz} / \overline{w(z)} \\ &= h^2 s. \end{aligned} \quad (7)$$

But as the selection gradient form is derived from the covariance form, it is not a fundamental part of the theory of natural selection that trait value underlies fitness value. It might well be that fitness arises from the phenotype in interaction with the environment, but the selection gradient description of selection tends to make us perceive this as the fundamental description of selection.

Robertson (1968) named expression (4) the Secondary Theorem of Natural Selection — the name “Fundamental Theorem” already being claimed for the special case that the trait is fitness itself. Caswell (1989: 163) rightly observes that the Secondary Theorem is more important than the fundamental theorem. In fact, it gives the most concise formulation of Darwin’s theory of natural selection that we have.

An important special case is the allele count (Price, 1970). The number of  $A_1$  alleles in an individual is  $x = 0, 1, \text{ or } 2$ . The average allele count is  $\bar{x} = 2p$ , where  $p$  is the allele frequency of  $A_1$ . Using genotypic values for fitness leads to

$$R = \Delta(2p) = \text{cov}\{x, w(g)\} / \overline{w(g)} \quad (8)$$

(Grafen, 1985), and as the heritability of allele count equals 1,

$$\Delta(2p) = \text{cov}\{x, w(z)\} / \overline{w(z)} \quad (9)$$

(Price, 1970), under the usual assumption of



linearity of fitness. One should, however, take care to realize that despite their similarity, there is one expression [i.e. (9)] for individual fitness, and another [i.e. (8)] for genotypic fitness. Allele frequency change itself can be written in terms of a covariance, between allele count and genotypic fitness, providing the link between the selection model in terms of genotype frequencies and fitness, and the selection model in terms of selection differential, heritability, and selection response.

The covariance approach generalizes fruitfully, and can be used to model allele frequency change owing to inclusive fitness. This was first done by Hamilton (1970), on the basis of the phenotypic version of Price's model [Eq. (9)]. Queller (1992) provides the genetic version of allele frequency change owing to inclusive fitness [i.e., starting with (8)], and explicates the difference between using the more general genetic form and the more restricted phenotypic form of the formulation of selection under inclusive fitness. The covariance selection model (8) provides a general framework to analyse kin selection and group selection in a subdivided population (Wade, 1985). Generalization of the genetic form of Price's model to more loci is possible (Nagylaki, 1989a). A generalization to more traits for the secondary theorem of natural selection is easily found by treating fitness itself as one of the traits in a multiple regression model. The vector of predicted changes in phenotypic means equals the genetic variance-covariance matrix of traits and fitness times the vector of selection gradients. As the selection gradients in such a multiple regression model pertain to the remaining variation, the vector values of selection gradients are 0 except for the selection gradient of fitness on itself, which equals 1 (van Tienderen, 1989). In such a model, fitness seems to be the trait on which natural selection acts (Christiansen, 1984).

#### DISCUSSION

What does "fitness" mean? The question is itself ambiguous. If we ask for numerical fitness definitions, the point is not whether some quantity is a good measure of some fitness while others are not, but what is a good model for the appropriate genotypic demography. What is fitness supposed to measure?

Some sort of overall performance or quality of design or aptness for life, or general adaptiveness? This seems to be a discussion that is standing outside the practice of evolutionary biology. What we usually ask is how such measures as individual lifetime reproductive success, expected lifetime reproductive success, net reproductive rate, reproductive value, demographic genotypic fitness, pair fitness, genotypic weights, growth rate of a population of the genotype of interest, and expected time to extinction are interrelated, and how they relate to the change in phenotypic traits. Given knowledge of the life history of the population, the causes and values of the fitness components, these relations can be spelled out in specific models. We need not ask whether expected time to extinction or genotypic weight is the proper fitness measure. What we would like to know is how they are related in a mechanistic model for a specified situation. If we knew that, what information would we gain from stating that one or the other is a "fitness measure"? This argues that it is not fruitful to dwell on the connotations of fitness from common English usage. Historically, the shift from fitness as used in common English to fitness as a technical quantity can be seen in Fisher's *The Genetical Theory of Natural Selection* (1930). In the paragraph on Natural Selection, Fisher writes: "Since  $m$  [the Malthusian parameter] measures fitness to survive by the objective fact of representation in future generations, the quantity  $pq\alpha$  will represent the contribution of each factor [i.e., allele in an asexual group] to the genetic variance in fitness" (p. 34). The first use of "fitness" in this sentence "fitness to survive" does not sound like a technical term at all, but the second time "fitness" is used, it is definitely a technical term. Actually, the genetic variance in the Malthusian parameter is given. If one attempts to summarize the genotypic demography in a technical fitness definition, the genotypic weights used in population genetics textbooks are suitable for describing the change in genotype frequencies in time. Consideration of the demography consequent upon a more complicated life history leads to the demographic genotypic fitness defined by line 6 in Table 2 (Charlesworth, 1980).

Even within this restricted focus of fitness

as a short-term genotypic weight useful for following genotypic demography, fitness proves not to be a trait: Fitness is not in any way a character that an individual might have, and this is an important conclusion from the models. Often we deal with one fitness component at a time, and this might appear to use individual fitness values just as we use individual trait values. The use of individual values for fitness components is predicated on the assumption that if all other components entering into fitness are equal, equality in the fitness component under attention will lead to equal overall fitness. This assumption has been shown to be invalid (de Jong, 1990); the identity of the genotype is also of importance, and the detail of the genotypic demography has to be spelled out. Fitness represents a *model* of all interactions within the population and of all pleiotropies of fitness components in shaping the demography of genotypes. The model leads to a summarizing value that only for simple cases coincides with any averaged individual feature, but might be greatly removed from anything observable on individuals. Neither is fitness a property of a genotypic cohort. This means that two often used measures, expected lifetime reproductive success and reproductive value at birth, are not identical to fitness, and are only numerically equal for certain specified situations. Reproductive success per time unit and survival between time units are relevant to fitness [cf. expressions (1)]. This means that it is highly relevant for our models of natural selection to understand how the variance in reproductive success should be attempted and what any model for the variance in lifetime reproductive success implies (see Brown, 1988; Barrowclough and Rockwell, 1993, for differing views on the variance in lifetime reproductive success and its relation to an underlying model; neither variance seems to be appropriate for demographic genotypic fitness). In sexually reproducing populations that do not form pairs and where the gametes combine at random, and in asexuals, fitness summarizes the numerical result of a genotype: We can justifiably speak of genotypic fitness. In a sexually reproducing population where fecundity is a property of the pair, fitness summarizes the numerical result of genotype combinations.

Nonhomogeneous interactions between individuals of the population moreover will influence fitness, as they influence the population growth rate.

The restriction of fitness to a demographic genotypic quantity has consequences for any model of the evolution of the mean of a phenotypic trait in a population. We have models for the change in the mean trait value in a population owing to genotypic fitness differences [Robertson (1968), Lande (1979), Iwasa et al. (1991)]. If fitness is due to genotypic interaction, models of the change in mean trait value seem to be absent. Pair fitness is usually treated as if male and female individual fitness can be defined and used. In the most basic form of the theory of natural selection, Robertson's Secondary Theorem (Robertson, 1968), genotypic fitness and genotypic value for the trait appear (4); this appearance of genotypic fitness is independent of the appearance of genotypic fitness from the demographic equations. Two independent lines of reasoning point to the priority of the genotypic formulation over the phenotypic formulation of selection. Individual fitness does not arise from the demographic equations. The well-known phenotypic form (5) of the prediction of the selection response is derived and approximate. The phenotypic or individual selection model is therefore more restricted than the genotypic selection model; this is also true for inclusive fitness (Queller, 1992).

On the basis of our models of genotypic demography and selection response, the role for the phenotype in natural selection seems to be that of an intermediate between genotype and fitness. Regardless of the extent to which natural selection might act on the phenotype, it is the resulting genotypic fitness that is of importance for the selection response. Selection is mediated by a covariance between the genotypic value for the trait and demographic genotypic fitness. Whether the phenotype is instrumental in shaping the genotypic value for fitness for the genotypic value for the trait [as in Fig. 1(a)], or whether the phenotype is accidental to the genotypic value for fitness, and gives rise incidentally to a genotypic value for the trait [as in Fig. 1(b)], is irrelevant to the formulation of the selection response in the trait as derived from the additive genetic

covariance between trait and fitness. The selection response for the trait is adequately represented by the additive genetic covariance between trait and fitness in both situations represented in Figure 1, but the description of the selection response by a selection gradient and heritability does not seem equally suitable for both situations. This has nothing to do with statistical or experimental procedure; that will be very much the same for both situations. The use of the selection gradient forces us to view phenotypic trait differences as the cause of fitness differences; a selection gradient of fitness on trait makes it difficult to think of fitness differences as the cause of differences in the phenotypic trait. The use of a genetic covariance does not introduce such a bias in our view: In a genetic covariance, causation between phenotypic trait differences and fitness differences can go either way, and its use prevents an undercurrent of an additional assumption about the direction of causation. A genetic covariance between trait and fitness can occur only through pleiotropy and linkage disequilibrium, the main process presumably being pleiotropy. The biological question becomes how the pleiotropy between trait and fitness arises, by selection from the environment, by common development, or both. The main focus for the study of natural selection would be the biological mechanisms leading to the covariance both when fitness arises from phenotype and environment, and when fitness develops together with the phenotype (Endler and McLellan, 1988).

The causes of fitness differences are often equated with differences in adaptation or adaptiveness. Reeve and Sherman (1993) define an adaptation as a phenotypic variant that results in the highest fitness, thereby precluding nonadaptive fitness differences. In the same vein, Byerly and Michod (1991) gave the name " $r$ -fitness" to the individually realized values of fitness components, and the name " $F$ -fitness" to the expected genotypic value for genotypic fitness. Byerly and Michod argued that differences in  $F$ -fitness were caused by differences in the adaptiveness of traits — what they called " $A$ -fitness." Both authors' views of the relation between adaptation and fitness seem to be germane to the selection gradient view. They seek the origin of fitness differences in the

interaction of phenotype and environment [as in Fig. 1(a)], where selection is blind to the underlying genotype. Adaptation, as a concept, seems to be tied to this view. Phenotypic differences lead to fitness differences, and explicitly (Reeve and Sherman, 1993) or implicitly (Byerly and Michod, 1991), fitness differences are used as a way to discern adaptation. Unfortunately, adaptation is not an easy concept to tie to the situation in Figure 1(b). If the phenotype is an associated trait [as in Figure 1(b)], it is not so clear in what sense the phenotype with the highest fitness should be the best adapted. If adaptation is demonstrated by observed conformity to a priori design specifications (Williams, 1992), it is not immediately obvious why size in insects should be an adaptation. Weight differences in *Callosobruchus maculatus* are associated with fitness differences, but the a priori design specifications are not clear. We seem to be forced to consider whether any situation as depicted in Figure 1(b) would lead to nonadaptive differences in the associated trait, despite the fitness differences. Differences in adaptation will lead to fitness differences, but fitness differences are not necessarily associated with differences in adaptation.

Byerly and Michod (1991), in rejecting innate suitability or good engineering design as a definition of fitness itself, precluded any possibility for a tautology between fitness and natural selection. Defining fitness as innate suitability or good engineering design would lead to fitness as the cause of differences in reproductive success; it would compel us to regard the covariance in Robertson's (1968) Secondary Theorem as the definition of fitness, in the nontechnical sense of fitness—and it would fuel the tautology discussion. Such a definition of fitness would seem to be more relevant to the second view presented in Figure 1. The two views of natural selection presented in Figure 1 might lead to different positions on the question of whether natural selection selects for anything but fitness.

It seems that Byerly and Michod (1991) deal with the causes of fitness differences within one environment, rather than with the causes of natural selection as do Wade and Kalisz (1990). The causes of natural selection over environments have to be distinguished from

the causes of fitness differences and phenotypic trait differences within one environment. The causal factor for natural selection can be identified by looking at the relationship between the selection gradient  $\beta$  and the environment, or at the relationship between the additive genetic covariance and the environment. A change in  $\beta$  or genetic covariance with the environment indicates the cause of selection (Clarke, 1975; Wade and Kalisz, 1990). The cause of selection on body size of willow leaf beetles can be identified by using a series of environments as predation (example in Wade and Kalisz, 1990), using the selection gradient  $\beta_{wz}$  in a clear example of selection according to the situation depicted in Figure 1(a). Using the selection gradient  $\beta_{wg}$ , in an example of selection according to the situation depicted in Figure 1(a), the cause of selection on amylase activity in *Drosophila melanogaster* can be identified by using the presence or absence of starch as alternative environments (de Jong and Scharloo, 1976). The cause of selection on adult body size in *Callosobruchus maculatus* can be identified as the changeover time of the cowpea weevil cultures (Sibly et al., 1991), using selection gradients  $\beta_{wz}$  in an example of selection according to the situation depicted in Figure 1(b). The analysis of the cause of natural selection proceeds in the same way, whether a phenotypic trait or a genotypic difference is used, or whether the situation is according to Figure 1(a) or according to Figure 1(b). But once the cause of natural selection is identified by experiments over a

range of environments, the causes of fitness differences within one environment remain as a subject of investigation. For the causes of fitness differences as for the causes of natural selection, the analysis requires a detailed knowledge of the ecology and all other aspects of the biology of the organism (cf. Endler, 1986), rather than just a detailed knowledge of the ecology of the organism (cf. Wade and Kalisz, 1990).

The fundamental statement about natural selection on a trait is the existence of a genetic covariance between trait values and fitness values. Trait values can be measured occasionally for a genotype, while demographic genotypic fitness values summarize a genotypic life history and its population background. This is a limited scope for the theory of natural selection, as seen against the wide background of philosophical arguments. Rejecting arguments for fitness as inherent suitability and for fitness differences as caused by trait differences, Ollason (1991) concluded that "all that can be achieved is a correlative relationship" between phenotype and fitness. In fact, all that can be achieved is a covariance between genotypic trait value and genotypic fitness. One can only conclude that Robertson's Secondary Theorem of Natural Selection should be accorded a central place in the theory of evolution by natural selection.

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APPENDIX 1

*Fitnesses for independent individuals*

Assume a population of sexual diploid individuals. Each individual survives independently from zygote to death. Mating is at random between gametes. Interactions between individuals in the population is homogeneous. Reproduction occurs several times at discrete points in time. At time  $t$ , the numbers of newly born of each genotype at a locus with two alleles  $A_1$  and  $A_2$ , with random mating between gametes independent of the age of the parents, and with equal viabilities and gamete production in males and females, become (see the Explanation of Symbols for notation):

$$\begin{aligned} n_{11,0,t} &= p_t (\sum_{x \geq 1} n_{11,x-1,t-1,q} p_{11,x-1} m_{11,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1,q} p_{12,x-1} m_{12,x}) \\ n_{12,0,t} &= q_t (\sum_{x \geq 1} n_{11,x-1,t-1,q} p_{11,x-1} m_{11,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1,q} p_{12,x-1} m_{12,x}) \\ &\quad + p_t (\sum_{x \geq 1} n_{22,x-1,t-1,q} p_{22,x-1} m_{22,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1,q} p_{12,x-1} m_{12,x}), \\ n_{22,0,t} &= q_t (\sum_{x \geq 1} n_{22,x-1,t-1,q} p_{22,x-1} m_{22,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x-1,t-1,q} p_{12,x-1} m_{12,x}). \end{aligned} \tag{A1}$$

Here  $p_t$  is the frequency of allele  $A_1$  in the paternal gametes, and  $q_t = 1 - p_t$ :

$$p_t = (\sum_{x \geq 1} n_{11,x,t,\sigma} m_{11,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x,t,\sigma} m_{12,x}) / (\sum_{kl} \sum_{x \geq 1} n_{kl,x,t,\sigma} m_{kl,x}). \tag{A2}$$

A fitness of females of age  $x$  with genotype  $A_1A_2$  giving rise to young of genotype  $A_1A_1$  could for instance be defined as (Taylor, 1990):

$$W_{12,x,11} \equiv \frac{1}{2} p n_{12,x,t,q} m_{12,x} / n_{12,x,t,q} = \frac{1}{2} p m_{12,x}. \tag{A3}$$

This fitness definition involves the probability of an allele of a given type going from the mother to the offspring, the probability of a given allele coming from males, and female fecundity. Instead of counting newborn at time  $t$  as in Eq. (A1), one might count adults just before reproduction at time  $t + 1$ :

$$n_{y,x,t+1} = n_{y,x-1,t} p_{y,x-1} \quad (x \geq 1). \tag{A4}$$

A fitness of females of age  $x$  at time  $t$  with genotype  $A_1A_2$ , giving rise to young of genotype  $A_1A_1$  surviving to age 1 at time  $t + 1$  and themselves surviving to age  $x + 1$  at time  $t + 1$ , could be then defined as (Taylor, 1990):

$$W_{12,x,11}'' \equiv (\frac{1}{2} p m_{12,x} m_{12,x} p_{11,0} + n_{12,x,t} p_{12,x}) / n_{12,x,t} = \frac{1}{2} p m_{12,x} p_{11,0} + p_{12,x}. \tag{A5}$$

Instead of the allele frequency  $p_t$ , male genotype frequency  $x_{y,t,\sigma}$  can be used. The fractional fitness  $W_{y,x,kl}'$  (Gregorius, 1984) of a female of age  $x$  with genotype  $A_xA_y$  is the number of her successful gametes from fertilizations by  $A_kA_l$  males:

$$x_{kl,t,\sigma} = \sum_{x \geq 1} n_{kl,x,t,\sigma} m_{kl,x} / \sum_{\sigma p} \sum_{x \geq 1} n_{\sigma p,x,t,\sigma} m_{\sigma p,x} \tag{A6}$$

$$W_{y,x,kl}' \equiv x_{kl,t,\sigma} n_{y,x,t,q} m_{y,x} / n_{y,x,t,q} = x_{kl,t,\sigma} m_{y,x}. \tag{A7a}$$

The fractional fitness of genotype  $A_xA_y$  with respect to genotype  $A_kA_l$  over all ages of females becomes

$$W_{y,kl}'' \equiv x_{kl,t,\sigma} \cdot (\sum_{x \geq 1} n_{y,x,t,q} m_{y,x}) / \sum_{x \geq 1} n_{y,x,t,q}. \tag{A7b}$$

Gregorius (1984) defines the gametic fitness  $W_y^g$  of a genotype as the average number of successful gametes produced by a member of that genotype, and the zygotic fitness  $W_y^z$  as the average number of zygotes produced by a member of that genotype:

$$W_y^z = \sum_{kl} x_{kl,t,\sigma} \cdot (\sum_{x \geq 1} n_{y,x,t,q} m_{y,x}) / \sum_{x \geq 1} n_{y,x,t,q}, \tag{A7c}$$

$$W_y^g = \sum_{kl \neq y} x_{kl,t,\sigma} \cdot (\sum_{x \geq 1} n_{y,x,t,q} m_{y,x}) / \sum_{x \geq 1} n_{y,x,t,q} + 2 \sum_{kl=y} x_{kl,t,\sigma} \cdot (\sum_{x \geq 1} n_{y,x,t,q} m_{y,x}) / \sum_{x \geq 1} n_{y,x,t,q}. \tag{A7d}$$

These fitnesses are average contributions to the newly born per adult.

The standard definition of demographic genotypic fitness equals the total contribution by a genotype to the gamete pool, divided by the number of newborn of the same genotype one time unit earlier:

$$w_{y,t-1} \equiv \sum_{x \geq 1} n_{y,x,t} m_{y,x} / n_{y,0,t-1}. \tag{A8}$$

For this demographic genotypic fitness, with random mating of gametes and equal fitness of males and females,

$$\bar{w}_{t-1} = p_{t-1}^2 w_{11,t-1} + 2p_{t-1}q_{t-1} w_{12,t-1} + q_{t-1}^2 w_{22,t-1}, \tag{A9}$$

$$n_{0,t} = n_{0,t-1}\bar{w}_{t-1}, \tag{A10a}$$

$$p_t = p_{t-1}(p_{t-1}w_{11,t-1} + q_{t-1}w_{12,t-1})/\bar{w}_{t-1}, \tag{A10b}$$

$$\Delta p = \frac{1}{2} p_{t-1} q_{t-1} d\bar{w}_{t-1} / dp_{t-1}. \tag{A10c}$$

Expression (A10b) is equivalent to equation (A2): The demographic fitness definition yields the genotypic weights.

With constant genotype frequencies and stable age distribution, the growth rate  $\lambda$  of the population is constant. From simplifying (A8), demographic genotypic fitness  $w_y$  becomes, independent of time,

$$w_y = \sum_{x \geq 1} \lambda^{-x+1} l_{y,x} m_{y,x}. \tag{A11a}$$

This is reminiscent of the expression for reproductive value at age  $x$ ; for a cohort in a population of one genotype,

$$v_x = (\lambda^x / l_x) \sum_{y \geq x} \lambda^{-y} l_y m_y \tag{A11b}$$

and reproductive value at birth would be, for one genotype within a cohort of a multiple genotype population,

$$v_{0,y} = \sum_{x \geq 1} \lambda^{-x} l_{y,x} m_{y,x}, \tag{A11c}$$

that is,  $w_y = \lambda v_{0,y}$ .

The form of demographic genotypic fitness  $w_y$  is equivalent to the form of reproductive value at birth for a cohort of that genotype, though the summation in demographic genotypic fitness is still over ages of organisms present at one time unit. In (A11a);  $\lambda$  refers to the growth rate of a population of all three genotypes, and depends upon the genotypic composition. The growth rate of a population of one genotype,  $A_i A_j$ , would be given by

$$1 = \sum_{x \geq 1} \lambda_y^x l_{y,x} m_{y,x}. \tag{A11d}$$

Here,  $\lambda_y$  in (A11d) is determined by the same age specific  $l_{y,x}$  and  $m_{y,x}$  as  $w_y$  in (A11a); this justifies the use of the growth rate of a population of a single genotype,  $\lambda_y = \exp(r_y)$ , or of the intrinsic rate of increase,  $r_y$ , as a measure of the fitness of a genotype if selection is density and frequency independent (Charlesworth, 1980).

With constant density,  $\lambda = 1$  and demographic genotypic fitness takes on the form of the net reproductive rate,  $R_0$ :

$$w_y = \sum_{x \geq 1} l_{y,x} m_{y,x}. \tag{A12a}$$

In the net reproductive rate  $R_0$  summation refers to a cohort over the ages of the cohort, and summation in  $w_y$  refers to the ages of all individuals present at one time. If all  $l_{y,x}$  or  $m_{y,x}$  are zero for  $x > 1$ , fitness  $w_y$  and net reproductive rate  $R_0$  are the same, whatever  $\lambda$ .

Lifetime reproductive success (LRS) can be observed over individuals. For any individual  $k$  of genotype  $ij$ , LRS becomes:

$$\text{LRS}_{y,k} = \sum_{x \geq 1} m_{y,x,k}. \tag{A12b}$$

The expected value of LRS over a genotypic cohort becomes

$$\text{LRS}_y = \sum_{x \geq 1} l_{y,x} m_{y,x}. \tag{A12c}$$

For mutant invasion, the pertinent population growth rate is that of the established genotype. A mutant can invade if

$$\sum_{x \geq 1} \lambda_e^{-x+1} l_{m,x} m_{m,x} > \sum_{x \geq 1} \lambda_e^{-x+1} l_{e,x} m_{e,x} = 1, \tag{A13}$$

which is true if  $\lambda_m > \lambda_e$ . The same criterion is valid for fixation of the mutant, when all of the population can be regarded as of the mutant genotype and the population growth rate can be held to be  $\lambda_m$ .

A simple and well-known case occurs when reproduction and adult survival are independent of age and density,  $m_{y,x} = m_y$ , and  $p_{x-1,y} = s_y$ , while juvenile survival to age  $x = 1$  differs from adult survival and might be density dependent,  $p_{0,y} = v_y$ . Then

$$w_y = v_y m_y / (1 - s_y / \lambda) \tag{A14}$$



and, for a population of one genotype:

$$\lambda_y = v_y m_y + s_y. \tag{A15}$$

At the equilibrium density of the population,  $\lambda = 1$ , and

$$w_y = v_y m_y / (1 - s_y). \tag{A16}$$

The form (A14) can be used to explain density-dependent selection or  $r$  and  $K$  selection. The form (A15) is often used in predictions in life history theory (Schaffer, 1974, 1979). It has to be remembered that it depends upon some assumptions about the life history, most importantly lack of interactions between genotypes.

For a population that is at the equilibrium number,  $\lambda = 1$  and net reproductive rate  $R_0$  and demographic genotypic fitness coincide. For a population that is fluctuating in number but on average does not increase or decrease,  $\lambda = 1$  but average  $R_{0,y}$  and average  $w_y$  do not coincide. It is not clear whether average  $R_{0,y}$  and average  $w_y$  always take the same ranking; average  $w_y$  is not necessarily a good predictor of the genotypic dynamics.

APPENDIX 2

*Fitnesses with pair interactions*

Demographic recurrence equations analogous to (1) for the number of newly born of each genotype can be written for the case that *individuals* mate at random in each mating season (Abugov, 1983, 1985, 1986; de Jong, 1982b). The number of eggs of a pair with a female  $A_k A_i$  of age  $x$  and a male  $A_k A_i$  equals  $F_{ykl,x}$ . All females mate once; males mate with a genotype specific rate  $m$ , until all females have mated. The effective number of males to the mating pool becomes

$$\bar{W}_\sigma = \sum_{kl} \sum_{x \geq 1} n_{kl,x,t} \sigma m_{kl}$$

and the frequency of matings by  $A_k A_i$  males becomes

$$x_{kl,t,\sigma} = \sum_{x \geq 1} n_{kl,x,t} \sigma m_{kl} / \bar{W}_\sigma.$$

The number of adults arriving at time  $t$  is, given the numbers leaving at time  $t - 1$ :

$$\sum_{x \geq 1} n_{y,x,t} = \sum_{x \geq 1} n_{y,x-1,t-1} \phi_{y,x-1}.$$

The numbers of newly born for each genotype are:

$$\begin{aligned} n_{11,0,t} &= \sum_{x \geq 1} n_{11,x,t} \phi x_{11,t,\sigma} F_{1111,x} + \frac{1}{2} \sum_{x \geq 1} n_{11,x,t} \phi x_{12,t,\sigma} F_{1112,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x,t} \phi x_{11,t,\sigma} F_{1211,x} \\ &\quad + \frac{1}{4} \sum_{x \geq 1} n_{12,x,t} \phi x_{12,t,\sigma} F_{1212,x}, \\ n_{12,0,t} &= \sum_{x \geq 1} n_{11,x,t} \phi x_{22,t,\sigma} F_{1122,x} + \sum_{x \geq 1} n_{22,x,t} \phi x_{11,t,\sigma} F_{2211,x} + \frac{1}{2} \sum_{x \geq 1} n_{11,x,t} \phi x_{12,t,\sigma} F_{1112,x} \\ &\quad + \frac{1}{2} \sum_{x \geq 1} n_{12,x,t} \phi x_{11,t,\sigma} F_{1211,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x,t} \phi x_{12,t,\sigma} F_{1212,x}, \\ n_{22,0,t} &= \sum_{x \geq 1} n_{22,x,t} \phi x_{22,t,\sigma} F_{2222,x} + \frac{1}{2} \sum_{x \geq 1} n_{22,x,t} \phi x_{12,t,\sigma} F_{2212,x} + \frac{1}{2} \sum_{x \geq 1} n_{12,x,t} \phi x_{22,t,\sigma} F_{1222,x} \\ &\quad + \frac{1}{4} \sum_{x \geq 1} n_{12,x,t} \phi x_{12,t,\sigma} F_{1212,x}. \end{aligned} \tag{A17}$$

It is possible to define a fitness for the genotypic combination in the pair as

$$w_{yhl,\text{pair}} = (\sum_{x \phi} \sum_{\sigma} n_{y,x,t,\phi} \cdot n_{kl,x,t,\sigma} m_{kl} F_{yhl,x}) / (n_{y,0,t-1,\phi} \cdot n_{kl,0,t-1,\sigma}) \tag{A18}$$

and a genotypic fitness of males, up to reproducing, as

$$w_{kl,\sigma} = \sum_{x \sigma} n_{kl,x,t,\sigma} m_{kl} / n_{kl,0,t-1,\sigma}. \tag{A19}$$

Mean pair fitness  $\bar{w}_{\text{pair}}$  is found by weighting the pair fitnesses by the frequencies of pairs of all genotypic combinations; mean male genotypic fitness by  $\bar{w}_\sigma$  weighting the male genotypic fitnesses by the genotypic frequencies of the male matings. The change in total numbers of newly born between two points in time becomes determined by  $\bar{w}_{\text{pair}}$  and  $\bar{w}_\sigma$ , in a way that actually emphasizes female fitness (Kempthorne and Pollak, 1970; de Jong, 1982b)

$$n_{0,t} = n_{0,t-1} \bar{w}_{\text{pair}} / \bar{w}_\sigma, \tag{A20}$$

while the change in allele frequency in the newly born becomes

$$\Delta p_{t-1} = \frac{1}{4} p_{t-1} q_{t-1} d \bar{w}_{\text{pair}} / d p_{t-1}. \tag{A21}$$

The growth rate of a population of one genotype becomes  $\lambda = w_{\text{pair}}/w_{\sigma}$ . To illustrate Abugov's (1985) result, let adult survival differ between males and females, and between genotypes, but be independent of age: for females,  $s_{y,\varphi}$ , for males  $s_{kl,\sigma}$ . With stable age distribution, stable polymorphism or weak selection, and constant growth rate of the population

$$w_{ykl,\text{pair}} = F_{ykl}v_{y,\varphi}v_{kl,\sigma}m_{kl}/[(1 - s_{y,\varphi}/\lambda) \cdot (1 - s_{kl,\sigma}/\lambda)] \quad (\text{A22})$$

and

$$w_{kl,\sigma} = v_{kl,\sigma}m_{kl}/(1 - s_{kl,\sigma}/\lambda). \quad (\text{A23})$$

A population of one genotype would grow at a rate of

$$\lambda = w_{\text{pair}}/w_{\sigma} = Fv_{\varphi}/(1 - s_{\varphi}/\lambda), \quad (\text{A24})$$

$$\lambda = Fv_{\varphi} + s_{\varphi}. \quad (\text{A25})$$

The growth rate of a population of one genotype (A24) cannot be used to predict pair fitness (A22).

### APPENDIX 3

#### *Covariances and selection gradients*

##### PHENOTYPIC SELECTION: FROM PHENOTYPIC AND GENOTYPIC SELECTION DIFFERENTIAL

In the usual model for a phenotypic trait  $z$  the trait value for an individual is determined by its genotypic value  $g$  and its environmental deviation  $e_z$ :  $z = g + e_z$ , with  $\bar{e}_z = 0$  so that  $\bar{z} = \bar{g}$ . The trait is assumed additive; dominance and epistasis are supposed to be absent in the trait, in order to make the expressions exact and not approximate.

Phenotypic selection on the individuals of a population is described by the phenotypic selection differential  $s$ , given the distribution of the trait in the population  $p(z)$  and the fitness function  $w(z)$ :

$$s \equiv [1/\overline{w(z)}] \int w(z) z p(z) dz - \bar{z}. \quad (\text{A26})$$

The definition of the selection differential shows that the product of the selection differential and mean phenotypic fitness is a covariance, the covariance between phenotypic value of the trait and phenotypic value of fitness:

$$\overline{w(z)}s = \text{cov}\{z, w(z)\}. \quad (\text{A27})$$

This allows us to define the phenotypic selection gradient for individuals as (Table 1):

$$\beta_{uz} \equiv \text{cov}\{z, w(z)\}/\text{var}\{z\} = \overline{w(z)}s/\text{var}\{z\} \quad (\text{A28})$$

(Iwasa et al., 1991). Categorizing the individuals per genotype, and using genotypic values for trait and fitness instead of the phenotypic values for trait and fitness per individual, permits us to define the genetic selection differential  $R$ . The genetic selection differential  $R$  becomes, given the distribution of genotypic values  $p(g)$  and the genotypic fitness function  $w(g)$ :

$$R \equiv [1/\overline{w(g)}] \int w(g) g p(g) dg - \bar{g}. \quad (\text{A29})$$

The definition of the genetic selection differential shows that the product of the selection differential and mean genotypic fitness is a covariance, the covariance between genotypic value of the trait and genotypic value of fitness:

$$\overline{w(g)}R = \text{cov}\{g, w(g)\}. \quad (\text{A30})$$

This allows us to define the genotypic selection gradient (Table 1):

$$\beta_{ug} \equiv \text{cov}\{g, w(g)\}/\text{var}\{g\} = \overline{w(g)}R/\text{var}\{g\} \quad (\text{A31})$$

(Iwasa et al., 1991), whatever the distribution  $p(g)$  of the genotypes and whatever the fitness values.

For additive gene effects within and between loci, the genetic selection response equals the genetic selection differential:  $\Delta\bar{g} = R$ ; and as the phenotypic mean equals the genotypic mean, the phenotypic selection response equals the genetic selection differential too:  $\Delta\bar{z} = \Delta\bar{g} = R$ . For a model of phenotypic selection, usually it is assumed that the phenotypic selection gradient and the genotypic selection gradient are the same, i.e., that  $\beta_{uz} = \beta_{ug} = \beta$ . Equating  $\beta_{uz}$  with  $\beta_{ug}$  leads to

$$\overline{w(z)s}/\text{var}\{z\} = \overline{w(g)}R/\text{var}\{g\} \tag{A32}$$

and if  $\overline{w(z)} = \overline{w(g)}$ , to

$$\Delta\bar{z} = \Delta\bar{g} = R = (\text{var}\{g\}/\text{var}\{z\})s, \tag{A33}$$

i.e., to the traditional  $\Delta\bar{z} = h^2s$ . Substituting  $\text{cov}\{z, w(z)\}$  for  $\overline{w(z)}s$  leads to  $\Delta\bar{z} = h^2\text{cov}\{z, w(z)\}/\overline{w(g)} = h^2\text{cov}\{z, w(z)\}/w(z)$  (Jacquard, 1977).

The assumption that the phenotypic selection gradient equals the genotypic selection gradient deserves attention. The fitness value of an individual with phenotypic trait value  $z = g + e_z$  can be found by a Taylor expansion around its genotypic value  $g$ :

$$w(z) = w(g) + e_z \cdot dw(z)/dz_{at\ g} + \frac{1}{2}e_z^2 d^2w(z)/dz_{at\ g}^2 + \dots + e_w. \tag{A34}$$

If  $e_z$  and  $e_w$  are independent of  $g$  and of each other and if the distribution of  $e_z$  is symmetric, the covariance of phenotype and fitness within this one genotype becomes

$$\text{cov}\{z - g, w(z) - w(g)\} = \text{cov}\{e_z, w(z) - w(g)\} = \text{var}\{e_z\} \cdot dw(z)/dz_{at\ g} + \mathcal{O}(e_z^4). \tag{A35}$$

The covariance over all genotypes becomes, where  $p(g)$  is the distribution of the genotypes,

$$\text{cov}\{z, w(z)\} = \text{cov}\{g, w(g)\} + \Sigma p(g)\text{var}\{e_z\}_{at\ g} \cdot dw(z)/dz_{at\ g}. \tag{A36}$$

For  $dw(z)/dz_{at\ g}$  to be the same for all  $g$ ,  $w(z)$  must be a linear function of  $z$ ; if  $w(z)$  is a linear function of  $z$ , it is likely that  $w(g)$  is a linear function of  $g$ , and that the regression  $\beta_{wg}$  equals the derivative  $dw(z)/dz$ . If we moreover assume that  $\text{var}\{e_z\}$  is the same for all genotypes, it follows that:

$$\text{cov}\{z, w(z)\} = \text{var}\{g\}\beta_{wg} + \text{var}\{e_z\}\beta_{wg} = \text{var}\{z\}\beta_{wg}, \tag{A37}$$

$$\beta_{wg} = \text{cov}\{z, w(z)\}/\text{var}\{z\} = \beta_{wz}. \tag{A38}$$

Linearity of the  $w(z)$  function is the condition for the two selection gradients to be equal, and therefore the condition for  $\Delta\bar{z} = h^2s$  to apply exactly rather than approximately.

PHENOTYPIC SELECTION: FROM POPULATION GENETICS

Another model for selection on a quantitative trait starts with the relation between selection response and gene frequency change and leads to a different formulation for the selection gradients. There is again both a genotypic and phenotypic selection gradient, but now in terms of the change of mean phenotypic fitness with mean phenotypic trait value or of mean genotypic fitness with mean genotypic trait value, instead of the change in phenotypic fitness with phenotypic trait value or of genotypic fitness with genotypic trait value.

The average effect of a gene substitution can be found as the regression of the genotypic values for trait or fitness on the allele count per genotype (Falconer, 1981); it can therefore be thought of as a constant converting allele count into additive value of the genotype for the trait. Under Hardy-Weinberg frequencies, such a regression is equivalent to half the change in mean genotypic value with the gene frequency (half, because of diploidy) (Kojima, 1959):

$$d\bar{g}/dp = 2\alpha_z. \tag{A39}$$

The average excess in fitness appears in  $\Delta p$ ; the average effect of a gene substitution is under Hardy-Weinberg frequencies equal to the average excess:

$$d\bar{w}/dp = 2\alpha_w. \tag{A40}$$

The mean genotypic value in the next generation of a trait coded for by a locus  $A$  with two alleles at allele frequencies  $p$  and  $q$  equals

$$\bar{g}_{t+1} = \bar{g}_t + \Delta p \cdot d\bar{g}/dp + \dots \tag{A41}$$

Neglecting higher-order terms, or exactly for an additive trait and arbitrary fitness,

$$\Delta\bar{g} = \Delta p \cdot d\bar{g}/dp = 2pq(\frac{1}{2}d\bar{w}/dp)(\frac{1}{2}d\bar{g}/dp)/\bar{w} \tag{A42a}$$

and therefore

$$\Delta\bar{g} = 2pq\alpha_z\alpha_w/\bar{w}. \tag{A42b}$$

The additive genetic covariance between trait value and fitness value owing to locus  $A$  equals  $2pq\alpha_z\alpha_w$ .

The change in mean genotypic value equals therefore the additive genetic covariance between genotypic value for the trait and genotypic fitness, divided by the mean genotypic fitness:

$$\Delta \bar{g} = \text{cov}_A(\text{trait}, \text{fitness}) / \overline{w(g)}. \quad (\text{A43})$$

Applying the chain rule for derivatives,  $d\bar{w}/dp = d\bar{w}/d\bar{g} \cdot d\bar{g}/dp$ , leads to

$$\begin{aligned} \Delta \bar{g} &= 2pq(\frac{1}{2} d\bar{w}/dp)(\frac{1}{2} d\bar{g}/dp) / \overline{w(g)} \\ &= 2pq(\frac{1}{2} d\bar{g}/dp)^2 \cdot (d\bar{w}/d\bar{g}) / \overline{w(g)} \\ &= V_A(g)(d\bar{w}/d\bar{g}) / \overline{w(g)} = V_A(g) \cdot \beta_{mu,mg} / \overline{w(g)}, \end{aligned} \quad (\text{A44})$$

where  $\beta_{mu,mg} \equiv d\bar{w}/d\bar{g}$  is a selection gradient, but now of mean fitness on mean genotypic value. The selection gradient  $\beta_{mu,mg}$  equals the selection gradient  $\beta_{ug}$  for a linear fitness function; otherwise, a Taylor approximation has to be used.

The phenotypic selection differential  $s$  can be related to a selection gradient  $\beta_{mu,mz}$  giving the change in mean phenotypic fitness owing to a change in mean phenotype. Lande (1979) showed by differentiation toward the phenotypic mean that for a normally distributed trait the selection differential equals  $s = \text{var}\{z\} \cdot d\overline{w(z)}/d\bar{z} = \text{var}\{z\}\beta_{mu,mz}$ , and by differentiation toward the mean of a normal distribution of genotypic values that the selection response equals  $\Delta \bar{g} = \text{var}\{g\} \cdot d\overline{w(g)}/d\bar{g} = \text{var}\{g\}\beta_{mu,mg}$  (to write his proof as it would appear for a single trait). The assumption of the identity of  $\beta_{mu,mz}$  and  $\beta_{mu,mg}$  takes in Lande (1979) the form of the assumption that  $d\overline{w(z)}/d\bar{z} = d\overline{w(g)}/d\bar{g}$ , i.e., that  $\nabla \ln\{\overline{w(z)}\} = \nabla \ln\{\overline{w(g)}\}$ . Again, any  $\beta_{mu,mz} \equiv d\overline{w(z)}/d\bar{z}$  only equals  $\beta_{uz} = d\overline{w(z)}/dz$  if the fitness function  $w(z)$  is linear; otherwise, a Taylor approximation has to be used. Linearity of the fitness function assures as before that  $\beta_{mu,mz}$  equals  $\beta_{mu,mg}$ . Therefore, this line of reasoning too leads to  $\Delta \bar{z} = h^2 s$  and its multivariate analog  $\Delta \bar{z} = GP^{-1}s$ .