



On the Assignment of Fitness Values in Statistical Analyses of Selection

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tained directional change in the optimum phenotype, a small amount of additive genetic variance always greatly reduces the total genetic load on the population. In contrast, with a cyclically fluctuating optimum, additive genetic variance significantly enhances population mean fitness only when the period of the oscillation is long and the amplitude is large. The situation is similar for positively autocorrelated fluctuations in the optimum: additive genetic variance is most effective in reducing the total load when the fluctuations exhibit a long autocorrelation time and high variance.

If one or more types of predictable environmental change occur simultaneously, additive genetic variance is more likely to diminish the total genetic load. Therefore, unless a population can remain in an environment to which it is preadapted by shifting its geographic distribution, for example, through habitat selection behavior (Pease et al. 1989), additive genetic variance and adaptive evolution can be critical for long-term population survival. With increasing habitat fragmentation and geographic isolation of populations caused by human activities, the maintenance of normal levels of additive genetic variance will become increasingly important as a mechanism of adaptation and population persistence in a changing environment.

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ON THE ASSIGNMENT OF FITNESS VALUES IN STATISTICAL ANALYSES OF SELECTION

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Recent advances in the statistical machinery available to analyze selection have resulted in a wealth of empirical studies seeking to understand and demonstrate the strength, mode, and importance of selection, both natural and sexual, in wild

populations. One of the primary limitations of data collected from natural populations is the inability to measure true lifetime fitness of multiple individuals (e.g., see Endler 1986). As the next best thing, researchers necessarily use some fit-

ness component as an indicator of total fitness. Although there are situations in which these variables are continuous, such as number of progeny (e.g., Kalisz 1986; Johnston 1991) or growth rate (e.g., Arnold 1988), often the fitness indicators are categorical measures such as alive/dead or mated/unmated, or ordinal measures such as number of years survived or number of mates. Such discrete measures are then assigned individual fitness values for statistical analysis to reveal the action of selection on the traits in question. Previous studies have investigated the statistical consequences of using discrete measures of fitness to estimate expected fitness functions (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). Herein, we examine how the specific numerical values assigned to individual fitnesses affect selection analyses.

Some of the most popular analytical techniques for detecting selection are based on regression, in which the characters of interest are used to predict fitness. Selection coefficients or surfaces are then estimable as functions relating the characters to fitness. It should be obvious that the numerical values of absolute fitness may affect the picture of selection obtained from the analysis. In particular, linear regression techniques including quadratic regression (Lande and Arnold 1983) and path analysis (Crespi and Bookstein 1989; Crespi 1990; Kingsolver and Schemske 1991) use partial regression coefficients as quantitative estimates of selection. Assignment of fitness values to categories of individuals is most likely to have an effect on such quantitative measures of selection, either inflating or deflating the interpreted strength of selection. The qualitative form of selection, in terms of direction, dips, and modes (though possibly not their exact position and certainly not their relative extremity) should still be accurately predicted by nonparametric regression (Schluter 1988; Schluter and Nychka 1994) and by quadratic regression when the surface truly is quadratic (but see Phillips and Arnold 1989; path analysis reveals only linear forms of selection in any case, Kingsolver and Schemske 1991).

The choice of numerical values for different individual fitness categories can be troublesome. It is certainly easy to justify the assignment of an absolute fitness of 0 to any individual dead or unmated during a study, but why assign those alive or mated an absolute fitness of 1, as opposed to some other number, say 10? Even more complicated categories may be sampled, for instance, survival to different ages (e.g., Scheiner 1989; Endler 1986). Biological intuition suggests assigning individuals that live longer a higher fitness because they have had more opportunities to reproduce, but exactly what values should be assigned? In studies of mating biology, the number of mates is typically used as a discrete measure of fitness (e.g., Arnold and Wade 1984a,b; Conner 1988; Hews 1990; Moore 1990; Anholt 1991; Madsen and Shine 1992, 1993), but is the true fitness difference between 3 and 4 mates equivalent to the difference between 0 and 1 (see e.g., Bateman 1948)? These are biological questions that only can be answered empirically for each system under study. Our purpose here is to investigate the effect of discrete measures of individual fitness on the estimation of several commonly reported selection coefficients to (1) reveal the conditions under which such calculations are robust to the

values chosen and (2) illustrate the need for strong biological reasoning in assigning numbers to fitness categories.

The Validity of Analyzing Discrete Categories of Fitness with Linear Regression

Linear regression techniques can be used to fit a curve to any type of dependent variable (Kendall and Stuart 1967; Lande and Arnold 1983), though this property is often misunderstood. Most of the commonly quoted assumptions of regression analysis, such as independent and normally distributed errors, pertain to significance testing, not to curve fitting (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). When the measure of fitness is discrete, alternatives to parametric significance testing must be used to evaluate the statistical significance of the selection coefficients obtained, but the numerical estimates and curve fits themselves will be valid. This issue has been dealt with in detail elsewhere (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). We will not address this topic except to note that a variety of options are available, including randomization and resampling techniques (e.g., Jayne and Bennett 1990; Mitchell-Olds and Shaw 1987; Brodie 1992), and generalized linear models, such as logistic or probit regression, to estimate the significance of models and terms (e.g., Smith 1990; Brodie 1992). We wish to stress that the use of linear regression techniques to analyze selection is not precluded when fitness is discrete or even binary. Coefficients from a least-squares linear regression analysis accurately describe the relationship between dependent (fitness) and independent (traits) variables (Kendall and Stuart 1967, ch. 18, 26). Although other forms of regression (i.e., generalized linear models) may provide better tests of significance for discrete dependent data (McCullagh and Nelder 1984), they do not yield coefficients of selection that plug directly into equations for phenotypic evolution (as does quadratic regression, Lande and Arnold 1983), nor do they provide path coefficients for evaluating causal pathways (as does path analysis, Kingsolver and Schemske 1991).

Coefficients of Selection

The most commonly reported coefficients of selection include the opportunity for selection, selection differentials, selection gradients, and path coefficients. Each of these differ in their biological and statistical interpretation (see Lande and Arnold 1983; Arnold and Wade 1984a; Phillips and Arnold 1989; Kingsolver and Schemske 1991). We will concern ourselves primarily with the calculation of these coefficients and how assigned values of absolute fitness affect each of them.

The opportunity for selection, I , describes the upper limit of the force of selection that can act on any trait (also referred to as "intensity of selection" and "index of total selection"; Crow 1958; Arnold and Wade 1984a). This parameter is measured as the variance in relative fitness

$$I = \frac{\sum (w - \bar{w})^2}{n}, \quad (1)$$

where w = relative fitness (see below), and n = number of individuals in the population.

The directional selection differential, s , measures the total selection acting on a trait, both direct and indirect, as the covariance between individual relative fitness and the trait, z ,

$$s = \frac{\sum(z - \bar{z})(w - \bar{w})}{n}. \quad (2)$$

Likewise, the stabilizing/disruptive and correlational selection differentials measure the total selection acting to change the variance of a trait or covariance between two traits. The covariance between relative fitness and the quadratic deviations of the character from its mean are used to measure these quadratic selection differentials (Lande and Arnold 1983; Phillips and Arnold 1989).

Selection gradients are measures of direct selection on a trait or combination of traits, independent of selection acting on measured correlated traits (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Phillips and Arnold 1989). As partial regression coefficients, directional selection gradients, β , are related to selection differentials by factoring in the matrix of phenotypic correlations, \mathbf{P} (Lande and Arnold 1983):

$$\beta = \mathbf{P}^{-1}s. \quad (3)$$

Path coefficients can describe the causal pathways of selection by considering an a priori hypothesis, the "path diagram" (Kingsolver and Schemske 1991). Both kinds of coefficients are obtained from linear regression analyses. The directional (β_i), stabilizing/disruptive (γ_{ii}), and correlational selection (γ_{ij}) gradients are easily calculated as the partial regression coefficients from a quadratic regression of individual relative fitness on the traits z_i and z_j

$$w = \alpha + \beta_i z_i + \beta_j z_j + \frac{1}{2} \gamma_{ii} z_i^2 + \frac{1}{2} \gamma_{jj} z_j^2 + \gamma_{ij} z_i z_j + \epsilon, \quad (4)$$

where an individual's trait is expressed as a deviation from the mean, $z = z - \bar{z}$ (Lande and Arnold 1983). Path coefficients are similarly obtained as coefficients from a series of multiple regressions in which the character data are standardized to a mean of 0 and standard deviation of 1 (Crespi and Bookstein 1989; Kingsolver and Schemske 1991).

Although these coefficients of selection differ in what aspect of selection they measure, each is some function of individual relative fitness. Therefore, to determine how assignment of absolute fitness values might affect the estimation of selection coefficients, we simply need to examine the relationship between discrete measures of absolute fitness and relative fitness. For any case in which relative fitness is independent of the values assigned to absolute fitness, all selection coefficients will be robust. In all other cases, changing the values assigned to absolute fitness will change the estimates of selection opportunity, differentials, gradients, and path coefficients.

The Case of Two Fitness Categories

An individual's relative fitness is simply its absolute fitness, W , divided by the mean absolute fitness of the population,

$$w = \frac{W}{\bar{W}}. \quad (5)$$

Assume that for a population studied, there are two categories of fitness (e.g., live and dead or mated and unmated). The frequency of individuals in the first category is p , and they are assigned an absolute fitness $W_A = A$, whereas the frequency of the second category is q , and they are assigned an absolute fitness $W_B = B$. The mean absolute fitness of the population is then

$$\bar{W} = pA + qB; \quad (6)$$

and the relative fitness of each category can be expressed as

$$w_A = \frac{A}{pA + qB}, \quad w_B = \frac{B}{pA + qB}. \quad (7A, B)$$

It is readily apparent that whenever one of the two categories is assigned an absolute fitness value of 0, relative fitness is independent of the absolute fitness of either class: the relative fitness of the 0 class is 0, and relative fitness of the second class becomes the inverse of the frequency of that class (for $A = 0$):

$$w_A = 0, \quad w_B = \frac{1}{q}.$$

Thus, any function derived from a regression analysis of individual relative fitness on any set of traits (i.e., gradients and path coefficients) will be unaffected by the specific values chosen for the second fitness category (as noted by Endler 1986, p. 186).

The variance of relative fitness, I , can be expressed (noting that the mean relative fitness is 1)

$$I = \frac{\sum(w - 1)^2}{n}. \quad (8A)$$

Assigning the above values to absolute fitness and simplifying, the opportunity for selection becomes

$$I = \frac{pA^2 + qB^2}{(pA + qB)^2} - 1. \quad (8B)$$

Under these conditions, the opportunity for selection will also be independent of the value of absolute fitness for the second category, and will be a function of the frequency of that category:

$$I = \frac{1 - q}{q}. \quad (8C)$$

Similar substitution into equation (2) yields the familiar form of the directional selection differential (e.g., Arnold and Wade 1984a)

$$s = \bar{z}_B - \bar{z}, \quad (9)$$

expressed as the difference between the phenotypic mean before and after selection (where \bar{z}_B is the mean after selection). In the case of two fitness categories, the mean of the non-zero class may be considered mean after selection.

These simplifications are true only when one of the two classes is assigned an absolute fitness of 0, as is common in mark-recapture studies of survivorship (e.g., Jayne and Bennett 1990; Smith 1990; Anholt 1991; Brodie 1992; Janzen 1993; King 1993), and mating success within a single episode (e.g., Arnqvist 1992). If one of the two fitness values is not

0, then there is no general solution, and each of the selection coefficients is directly affected by the values chosen.

The Case of Three or More Fitness Categories

When multiple categories of fitness are measured, such as individuals recaptured at several ages, or acquiring varying numbers of mates, it is intuitively desirable to include these apparent differences in fitness in an analysis of selection. By examining just the case of three categories, we can see how important the values of absolute fitness assigned become. Building on the two category case, we add a third class of individuals that occurs at frequency r , and assign them an absolute fitness $W_C = C$. The average absolute fitness of the population now becomes

$$\bar{W} = pA + qB + rC, \quad (10)$$

and the relative fitnesses of the three classes become

$$\begin{aligned} w_A &= \frac{A}{pA + qB + rC}, \\ w_B &= \frac{B}{pA + qB + rC}, \\ w_C &= \frac{C}{pA + qB + rC}. \end{aligned} \quad (11A, B, C)$$

The variance in relative fitness, or opportunity for selection is

$$I = \frac{pA^2 + qB^2 + rC^2}{(pA + qB + rC)^2} - 1. \quad (12)$$

Because of the addition of the third category, even assigning an absolute fitness of 0 to one of the classes does not simplify these formulas. Relative fitnesses of the non-zero classes will be mutually dependent on the other's assigned absolute fitness, as will the variance of relative fitness. Thus, whenever more than two classes of individuals are analyzed, selection coefficients will directly reflect the values chosen for absolute fitness.

An Example: Laboratory Survivorship in Painted Turtles

To illustrate the impact of different assigned fitness values, we present an actual data set of laboratory survival of painted turtles (*Chrysemys picta*) hatched in captivity. These data were collected during the course of another study on the ecological significance of temperature-dependent sex determination, and details of collection (Janzen 1994) and husbandry (Janzen 1995) can be found therein. For the purpose of this example, it is important to note that eggs were collected from the wild in June of 1989 and were incubated and hatched in the laboratory at the University of Chicago. Carapace length, a measure of body size, was measured for each individual at hatching. From March to November (August to November in the first year), all individuals were held in a $3 \times 3 \times 1$ m outdoor concrete pond, enclosed to prevent emigration of the turtles or intrusion by predators. Each winter, turtles were removed from the pond and hibernated indoors in water at 5°C.

Survivorship was assessed monthly for 4 yr. Such survi-

TABLE 1. Coefficients of selection estimated using different values of absolute fitness. Data used are laboratory survivorship of painted turtles as a function of hatchling body size.

Case	Fitness	Differential	Opportunity
A	0, 1	0.454	1.88
B	0, 4	0.454	1.88
C	1, 2	0.117	0.13
D	0, 1, 2, 3, 4	0.228	0.45
E	1, 2, 3, 4, 5	0.158	0.22
F	0, 1, 2, 3, 8	0.315	0.82

vorship data present several options for examining the relationship between hatchling size and survival. Survival could be treated as a two-state variable, either alive or dead at the end of the study, and this information could be coded in several ways (Table 1, cases A–C). A more continuous measure of survival could be adopted, scoring the number of years survived (Table 1, cases D, E). It is even arguable that survival beyond the fourth year is much more important because this is the approximate age of reproductive maturity for painted turtles in Illinois (Moll 1973) (Table 1, case F). In any of these cases, the exact values assigned for absolute fitness are arbitrarily chosen. For the two category cases, we chose 0/1, 0/4, and 1/2 as the fitnesses of individuals dead and alive (respectively) at the end of the study. In the more continuous, and intuitively more pleasing, measure of survival, individuals were assigned fitnesses equal to the number of summers survived (Table 1, case D). In case E, these values were increased by one, and in case F, those individuals living to reproductive maturity were assigned a fitness twice their age ($W = 8$).

These data were then used to estimate the standardized directional selection gradient (based on character data standardized to a mean of 0 and a variance of 1, Lande and Arnold 1983) on body size for these turtles, using a linear regression and jackknifing for significance tests (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). In the univariate case, selection gradients and differentials are equivalent. The opportunity for selection was also estimated for each case.

The estimated standardized selection gradients on body size for this study span a nearly $4 \times$ range depending on the values of absolute fitness assigned. Each of the estimates is statistically significant ($P < 0.001$), but the quantitative differences lead to vastly different conclusions about the strength and importance of selection. The largest gradient, estimated from 0, 1 (and 0, 4) fitness values, suggests a change in mean body size of almost half a standard deviation due to selection. At the other extreme, fitness values of 1, 2 yield an estimated gradient that describes a change of little more than one-tenth of a standard deviation. Opportunities for selection are even more seriously affected, with more than an order of magnitude separating the largest and smallest estimates. Note that for both the gradients and the opportunities for selection, estimates were the same when there were only two fitness categories, one of which was 0.

Analyzing Discrete Fitness Categories

It should be clear that, although appropriate (Kendall and Stuart 1967; Lande and Arnold 1983; Mitchell-Olds and

Shaw 1987), discrete measures of fitness or fitness components present special problems for selection analysis. Discrete data can be analyzed using common linear regression based approaches, but the numerical values assigned to individual fitnesses will effect the quantitative estimates of selection obtained. Although continuous measures of lifetime fitness are ideal, natural systems and the logistics of data collection often dictate that only discrete measures of fitness components can be obtained. The challenge is to assign numerical values of individual fitness that will allow meaningful biological conclusions.

Selection gradients and differentials and path coefficients are actually estimates of a relationship between phenotype and the expected fitness of an individual with a particular trait value (see Lande and Arnold 1983). These are calculated based on actual individual fitness values. Empirical biologists analyzing selection must then assign individual fitnesses that reflect expected fitness. An example of the difference between these two types of fitness is the number of mates that a male acquires. Empirically, one can record males that acquire 0, 1, 2, 3, or more mates (individual fitness), yet the expected fitness of a male with a given phenotype may be 2.7 mates. Obviously, no male can acquire fractional mates; thus, it is impossible to measure an individual fitness that is equal to the expected fitness. Similarly, with survivorship data individuals either live or die, yet expected fitness is expressed as a continuous probability of survival (e.g., Schluter 1988; Brodie 1992).

Assigned values of individual fitness should be chosen to reflect expected fitness. Take, for example, Bateman's (1948) classic data on the relationship between number of mates and number of offspring in male and female *Drosophila*. For males, the number of offspring produced increases with the number of mates, whereas for females the relationship is asymptotic—more than one mate rarely translates to additional offspring. If one sought to analyze selection on a potential correlate of mating success, the intuitive fitness value might be number of mates. Although this measure of individual fitness would be appropriate for males, it would lead to inaccurate conclusions about the strength of selection on the character in females, because additional mates do not usually increase a female's fitness.

One way around this problem is to partition a selection analysis into episodes corresponding to major components of fitness (Arnold and Wade 1984a,b). This approach treats fitness of each episode as multiplicative, leading to additive selection coefficients that only refer to a given episode. In the Bateman (1948) example above, one would have separate estimates for mating success and for number of offspring per mate. Thus, it would be appropriate to assign females individual fitnesses equal to number of mates, because this would then be factored by the number of offspring per mate (cf., Arnold and Wade 1984b). The fitness component measured in discrete units would be related to expected fitness through the next episode. Unfortunately, biologists are often presented with systems in which it is impossible to collect data on multiple episodes of selection; thus, the partitioning approach cannot be adopted. Nonetheless, this kind of thought process should lead to the values assigned for individual

fitness categories when multiple episodes cannot be measured.

Quantitative estimates of the strength and form of selection, especially in combination with nonparametric analyses of the shape of the selective topography (Schluter 1988; Schluter and Nychka 1994), provide important insights into the process of evolution within populations. Discrete measures of fitness components are sometimes the best data that can be practically obtained from natural systems, but even these can be analyzed using common techniques. Because the numerical values of individual fitnesses effect the selection coefficients obtained, it is crucial to assign biologically relevant values. Caution must be applied when interpreting these coefficients, because they are not based on lifetime fitness.

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HERITABILITY OF WING LENGTH IN NATURE FOR THE MILKWEED BUG, *ONCOPELTUS FASCIATUS*

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The relationship between laboratory estimates of heritability and heritability in nature is an important issue for our understanding of evolutionary change and maintenance of genetic variation (Coyne and Beecham 1987; Riska et al. 1989; Prout and Barker 1989). When investigated in laboratory environments, many traits, even some closely related to fitness, have moderate to high heritability (Roff and Mousseau 1987; Mousseau and Roff 1987). At present, we have little idea whether these same traits would have moderate to high heritability in nature, but there are reasons to suspect bias in laboratory estimates. Minimizing environmental variation in the laboratory facilitates detection of genetic variation but also results in heritabilities that are likely to be greater than they would be in nature. If there is genotype \times environment ($G \times E$) interaction between the laboratory and natural environments, estimates of additive genetic variance obtained in the laboratory are likely to be biased; they could either underestimate or overestimate additive genetic variance in nature (Gupta and Lewontin 1982). There are a num-

ber of reasons why it is important to determine if laboratory studies provide reasonably unbiased estimates of heritability in nature. If heritabilities in nature tend to be considerably lower than laboratory estimates, lack of expressed genetic variation could be a reasonable general explanation for cases in which evolution fails to occur despite apparent selection pressure (Bradshaw 1991). In addition, low heritabilities may be accounted for parsimoniously by a balance between mutation and stabilizing selection, a process that does not appear capable of explaining the moderate to high heritabilities often found in laboratory studies (Barton 1990). Alternatively, if heritabilities are as high in nature as implied by laboratory studies, it will continue to be necessary to investigate factors other than lack of genetic variation to account for evolutionary stasis (Bradshaw 1991) and to assess the relative contributions of various forms of diversifying selection to explain the maintenance of substantial heritable variation in nature (Stearns 1992).

Unfortunately, for many species it is not practical to measure heritability in nature, especially for highly mobile species in which emigration from the natal environment is an essential feature of the life history. An alternative is to use information from field-collected parents and laboratory-

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