



On the Measurement of Natural and Sexual Selection: Applications

Stevan J. Arnold; Michael J. Wade

Evolution, Vol. 38, No. 4 (Jul., 1984), 720-734.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198407%2938%3A4%3C720%3AOTMONA%3E2.0.CO%3B2-2>

Evolution is currently published by Society for the Study of Evolution.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

ON THE MEASUREMENT OF NATURAL AND SEXUAL SELECTION: APPLICATIONS

STEVAN J. ARNOLD AND MICHAEL J. WADE

Department of Biology, University of Chicago, Chicago, Illinois 60637

Received October 27, 1981. Revised December 17, 1983

In this paper, we use measures of selection developed by quantitative geneticists and some new results (Arnold and Wade, 1984) to analyze multiple episodes of selection in natural populations of amphibians, reptiles, and insects. These examples show how different methods of data collection influence the potential for relating field observations to formal evolutionary theory.

We adhere to the Darwinian tradition of distinguishing between natural and sexual selection (Darwin, 1859, 1871; Ghiselin, 1974). We view *sexual selection* as selection arising from variance in mating success and *natural selection* as arising from variance in other components of fitness. The justification for this formal distinction is developed by Wade (1979), Lande (1980), Wade and Arnold (1980), Arnold and Houck (1982) and Arnold (1983a). (We define *mating success* as the number of mates that bear progeny given survival of the mating organism to sexual maturity. We do *not* equate mating success with mere copulatory success.) The utility of the distinction between sexual and natural selection is that the two forms of selection may often act in opposite directions on particular characters (Darwin, 1859, 1871). While we find the distinction between these two forms of selection useful, the difference is not crucial to our analysis. The essential point is that the recognition of selection episodes permits analysis of selection that may change in magnitude and direction during the life cycle.

Defining Fitness Components.—The key first step in the analysis of data is to define multiplicative components of fitness so that selection can be partitioned into parts corresponding to these com-

ponents or episodes of selection. Using an animal example, if the number of offspring zygotes is taken as total fitness, we can define the following components of fitness: viability (survivorship to sexual maturity), mating success (the number of mates) and fertility per mate (the average number of zygotes produced per mate). These components of fitness are defined so that their product gives total fitness. As a second example, consider the components of fitness in a plant in which yield (seeds/plant) is taken as the measure of total fitness (Primack and Antonovics, 1981). We might define the following components of fitness: number of stems per plant, average number of inflorescences per stem, average number of seed capsules per inflorescence, and average number of seeds per capsule. Again, these four fitness components are defined so that their product gives total fitness.

We will need to measure each component of fitness and each character on each individual in order to partition selection into parts corresponding to the separate episodes of selection or to the separate components of fitness. Thus in the animal example, we need to measure the viability, mating success and fertility of each individual. With this accomplished we can estimate the separate forces of viability, sexual and fertility selection on each phenotypic character. In addition we can calculate the opportunities of selection corresponding to these three episodes and covariances between the different kinds of selection.

In the plant example, we might begin with the intuition that larger plants have a greater yield. Using our methodology we can reword and extend this intuition. We can not only test the proposition of

size-dependent yield, but also measure the total force of selection on plant size. Furthermore we can ask whether size-dependent yield arises because larger plants have more stems, more inflorescences, more capsules, or more seeds. Re-wording the question, we can ask which parts of the plant contribute to selection on plant size and we can measure these separate forces. Finally we can recognize that correlations between numbers of plant parts (e.g., the covariance between number of stems and the average number of inflorescences per stem) constitute parts of the total opportunity for selection in the plant population.

In defining fitness components or a sequence of selection episodes we must be careful not to cross from one generation into the next. The reason for this rule is that in equations for evolutionary change total fitness is defined as the number of zygotes produced by a particular zygote (Crow and Kimura, 1970). If total fitness is measured starting at any other point on the life cycle, selection can be seriously misrepresented (Prout, 1965). So long as we remain within a generation in tallying total fitness or part of it, selection will not be confounded with inheritance. Thus if we begin to tally fitness at sexual maturity and take the number of progeny that reach sexual maturity as our measure of total lifetime fitness, we will confound fitness of parents (e.g., fertility) with the inheritance of fitness in their progeny (e.g., viability). This definition of fitness may be common in practice but it has a serious drawback. Fitness measured across generations cannot easily be related to formal evolutionary theory. If fitness is tallied within a generation, selection and inheritance can be conveniently treated as separate issues and we can model the evolutionary response to selection.

Fitness Need Not be Normally Distributed.—Fitness and its components often show conspicuous departures from normality (Wright, 1968). Such departures from normality do not affect the results in this paper. (The one exception is exp.

(20) [Arnold and Wade, 1984] which assumes a multinormal distribution of fitness components.) It is appropriate to characterize a distribution by its mean and variance irrespective of normality. Likewise, the partitioning of variance employed here and in Wade (1979) and Wade and Arnold (1980) does not depend on an assumption of normality (Brownlee, 1965). This assumption does come into play in tests of significance of differences in variance that depend on the F distribution. There are two avenues of analysis available if such significance testing is of primary interest and distributions are markedly non-normal: parametric statistical tests after transformation of scale to approach normality, and nonparametric statistical tests. In this paper, however, we are concerned primarily with the estimation and partitioning of variances and covariances and not with tests of significance. When the aims are to measure selection and relate the estimates to evolutionary theory, one should not attempt to transform fitness so that it has a normal distribution. In contrast, normality of characters other than fitness is highly desirable. For further discussion of the assumption of normality in measurement of selection see Lande and Arnold (1983).

Cross-Sectional Versus Longitudinal Data.—There are two distinct ways to collect data that are commonly used in empirical studies of selection. In the *longitudinal* approach individuals are followed through time and assigned fitnesses on a scale that usually consists of more than two categories. In the *cross-sectional* approach the population is sampled at a particular point in time. Individuals are not followed through time and there may be only two fitness categories (e.g., alive versus dead, or mated versus unmated).

Longitudinal data are more desirable than cross-sectional data since they impose fewer limitations and their interpretation requires fewer assumptions (Lande and Arnold, 1983). The critical assumption that must be made with cross-sectional data is that the relative fitnesses

of a particular phenotypic class are representative and can be extrapolated from the brief sample period to some longer interval in the life cycle. Thus if mating success varies in some systematic way during the breeding season (e.g., smaller males are more successful early in the season), longitudinal data will give accurate estimates of seasonal mating success but cross-sectional estimates, made from some short time interval, may seriously over- or underestimate seasonal success.

Furthermore, cross-sectional data cannot be used to estimate selection on characters that change with age. This limitation of cross-sectional data arises because individuals in the population may show different growth trajectories. Only with longitudinal data can we disentangle the effects of growth (or ontogenetic change) and selection. Thus if we have only cross-sectional data that show that larger individuals have larger harems, selection may have favored larger size at all size at all ages but it is also possible that larger individuals may have accumulated more mates simply because they are older and there may have been no selection on size per se. We can distinguish between these possibilities only with longitudinal data (additional complications arising from ontogeny are discussed below).

In order to make unbiased estimates from longitudinal data it is essential that all individuals be sampled (observed) at random in the event that it is impossible to record all or virtually all events that occur. Altmann (1974) provides an excellent discussion of solutions to such behavioral sampling problems.

In cross-sectional analysis of sexual selection, the population is sampled during a particular short interval of time and individuals may simply be classified into mated and unmated fractions. For example, sizes of male frogs are recorded for males in amplexus and for solitary males on a single evening during the mating season. In order to test the hypothesis that the two fractions differ in size or

some other attribute, it is convenient to test for a difference in the means of the two fractions using analysis of variance, *t*-test or appropriate nonparametric tests. This is the commonest form of data analysis in the current sexual selection literature. However, in order to estimate the magnitude of sexual selection as a parameter, rather than simply test the hypothesis of its presence or absence, we desire the difference in mean before and after selection. This selection differential can be calculated by taking the mean of mated males and subtracting the mean of all males (pooling the mated and unmated fractions). Consequently, in order to accurately estimate the sexual selection differential from cross-sectional data, it is essential to sample mated and unmated males in proportion to their actual representation in the population. In contrast, nonsystematic samples of the two fractions with greater effort generally devoted to the rarer fraction often suffice for hypothesis testing but not for parameter estimation.

Complications Arising from Age Structure.—A simple progeny count is not the appropriate measure of fitness if the population has age-structure (generations overlap in time) and is changing in size (Charlesworth, 1980; Lande, 1982). In such age-structured, nonstationary populations fitness must be measured by adjusting each individual's progeny count by the growth rate of the population. Lande (1982) derives selection differential and gradients for such populations. The selection measures used in this paper are most appropriate if the population has discrete generations or is stationary.

Complications Arising from Ontogeny.—Characters that change during ontogeny introduce an additional complication. Lande (1982) discusses two approaches. First, characters can be defined so that they are age-specific and hence actually or virtually invariant for an individual at a particular age or ontogenetic stage (e.g., the size of a three year old male or larval gill raker number). If there are very many morphometric

characters or age classes to be recognized, a second approach is to use statistical estimates of the growth parameters of individuals as characters rather than the character measurements per se. Thus with longitudinal data and appropriate transformation of character scale it may be possible to describe the ontogenetic trajectories of individuals with only few parameters (Cock, 1966). For example, if body size is transformed so that the regression on age is linear, then the regression and slope intercept can be used as characters that together describe size at any age. In this instance we would separately calculate the selection differentials or gradients of regression intercept and slope. This would also be an excellent approach for behavioral attributes that vary with temperature (e.g., mating call parameters in frogs and crickets). These could be regressed on temperature and the regression parameters of individuals could then be used as characters. The most prevalent current practice is to assume that all individuals fall on the same regression or at least have the same slope: assumptions that can be easily verified with longitudinal data. Linear regression is merely a convenience. The coefficients for any family of curves that describe individual variation could be used as characters (e.g., Atchley and Rutledge, 1981).

EXAMPLES OF DATA ANALYSIS

We have several goals in this section. One goal is to make abstract concepts of selection more tangible by using actual examples. A second goal is to illustrate the actual calculations used in data analysis. A third goal is to consider how limitations of the data can constrain evolutionary interpretations. Finally we point out the advantages of our methodology over other forms of data analysis prevalent in the literature.

An Example of Data Analysis with Longitudinal Data and Three Intercorrelated Selection Episodes.—Howard's (1979) study of reproductive success in bullfrogs (*Rana catesbeiana*) provides an

example of longitudinal data, as well as an example of successive episodes of selection, that will be analyzed here with the techniques outlined in Arnold and Wade (1984). Howard followed 38 individually-marked male frogs throughout a breeding season and recorded for each male the number of mates, the total number of zygotes per mate (clutch size per mate) and the total number of zygotes that hatched per clutch (Table 1). These aspects of total fitness can be viewed as three successive episodes of selection: sexual selection (mating success, W_1), followed by two episodes of natural selection (fertility per mate, W_2 , and egg hatching success, W_3). The product of these three fitness components, W , is total fitness or the number of tadpoles sired by the male. Howard suspected that selection for large male body size occurred through all three components of fitness. He noted that larger males mated with more females and, because he found positive assortative mating for size, with larger females producing larger clutches, he proposed that larger males sired more offspring per mate. Furthermore, because larger males controlled better territories for embryonic development, he also proposed that larger males had greater per capita hatching success. We will test these propositions and estimate the relative contributions of each episode to selection on male size.

It is useful to arrange the data for calculation, as in Table 1, with columns representing the running products of fitness components (W_1 , W_1W_2 , $W_1W_2W_3$) rather than with columns representing the separate components (W_1 , W_2 , W_3). This arrangement avoids redundant multiplication and hence rounding errors. In the calculations each individual is weighted by its fitness in preceding selection episodes. The weights or abstract frequencies, p_1 and p_2 , are also shown in Table 1 to emphasize the point that the weight attached to each individual data point changes with each episode of selection. Thus $p_1 = w_1/38$ is the weight attached to an individual after the first selection

TABLE 1. Reproductive success in a population of 38 male bullfrogs (*Rana catesbeiana*) studied by Howard (1979).*

Male body size (mm)**	Number of mates \bar{W}_1	Number of zygotes $\bar{W}_1\bar{W}_2$	Number of hatchlings $\bar{W}_1\bar{W}_2\bar{W}_3$	Phenotypic frequencies	
				P_1	P_2
144	3	44,518	20,842	.1111	.1051
150	2	59,035	29,377	.0741	.1393
144	1	9,385	1,923	.0370	.0222
154	1	7,309	4,014	.0370	.0173
132	1	7,309	3,356	.0370	.0173
148	1	21,498	18,325	.0370	.0507
143	1	23,278	13,506	.0370	.0549
144	1	19,821	14,951	.0370	.0468
146	1	15,862	7,113	.0370	.0374
134	1	14,092	2,062	.0370	.0333
143	2	14,459	9,924	.0741	.0341
138	1	4,928	2,194	.0370	.0116
141	3	47,957	26,041	.1111	.1132
122	1	10,709	299	.0370	.0253
134	1	9,899	3,418	.0370	.0234
138	2	47,736	19,169	.0741	.1127
145	1	25,819	23,198	.0370	.0609
128	1	22,673	5,074	.0370	.0535
119	1	7,738	2,578	.0370	.0183
125	1	9,640	4,760	.0370	.0228
141, 114, 121,					
148, 115, 117,					
132, 114, 95,					
133, 114, 114,					
142, 128, 137,					
125, 112, 112					
$\bar{z} = 4.871$	$\bar{W}_1 = .7105$	$\bar{W}_1\bar{W}_2 = 11,149.079$	$\bar{W}_1\bar{W}_2\bar{W}_3 = 5,582.2105$	$\Sigma = 1.0000$	$\Sigma = 1.0000$
$P = .012$	$V_{W_1} = .698$	$V_{W_1W_2} = (15,720.215)^2$	$V_{W_1W_2W_3} = (8,534.189)^2$		
	$I_1 = 1.382$	$I_{12} = 1.988$	$I = 2.337$		

* When using the formulae of Arnold and Wade (1984) to calculate variances and covariances in Tables 1-7, substitute $n - 1$ for n .
 ** The reported mean and variance, \bar{z} and P , are for the natural logarithms of male body size.

episode. It is not necessary to actually tabulate these frequencies for calculation since they can be generated as needed from the other columns using expression (4) in Arnold and Wade (1984).

It is useful to review the limitations imposed by the data before trying to interpret the results. Howard straddled two generations in defining total fitness (mating success is an attribute of the parent, but hatching success is an attribute of offspring). In addition total fitness pertains only to a breeding season and is not total lifetime fitness. These two limitations will mean that the calculated total selection opportunities and differentials will actually represent only part of the actual totals and cannot easily be related to evolutionary theory. Furthermore since the bullfrog population has age-structure rather than discrete generations and may be nonstationary, total fitness should have been measured in relation to the growth rate of the population (Lande, 1982) rather than as a simple progeny count. In addition the interpretation of the calculated selective forces on male body size is complicated by the fact that size increases during ontogeny. Furthermore, since only one character was scored (body size) we cannot separate direct selection on size from indirect selection on phenotypically correlated characters.

By dwelling on the limitations of Howard's data, we are not deprecating his study, for there are many admirable features (e.g., he could unambiguously determine the sire of each zygote). The limitations of the bullfrog data are common to many empirical studies and we point them out to illustrate the problems that are likely to confront many analyses of selection. The best strategy is to clearly recognize the limitations imposed by the data and qualify the interpretations accordingly, as Howard did.

In Howard's (1979) bullfrog population, sexual selection generated the major selective force favoring large male body size (Fig. 1, Table 2). Sexual selection accounted for 75% of the total selection

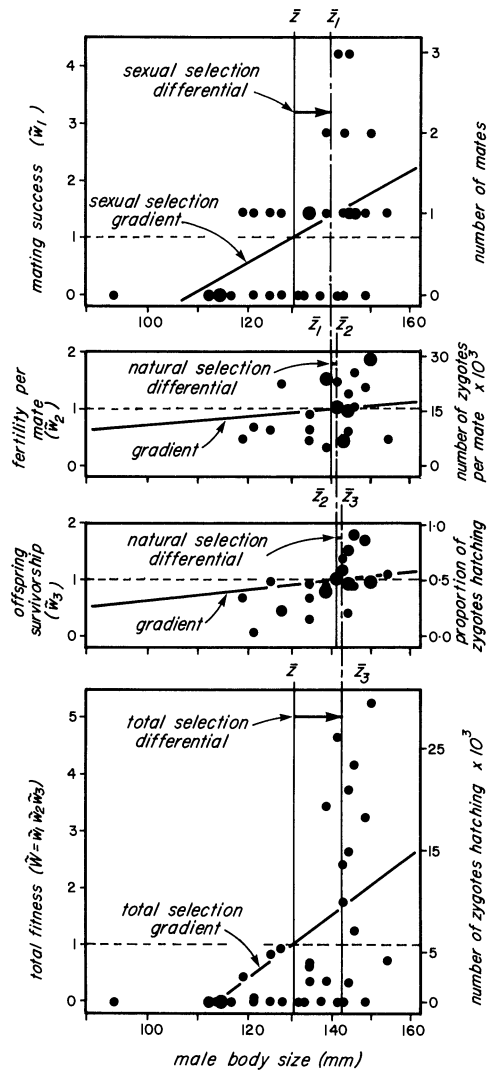


FIG. 1. A graphic analysis of Howard's (1979) data on three episodes of selection acting on a population of male bullfrogs (*Rana catesbeiana*). The top three panels show three components of fitness (mating success, fertility per mate and offspring survivorship) as functions of male body size. Total fitness, the product of the three fitness components, is shown as a function of body size in the bottom panel. Relative fitness is indicated on the left side of each panel; absolute fitness is shown on the right side. Notice that both selection differentials (shifts in mean) and selection gradients (least squares regressions of relative fitness on body size) corresponding to the three separate episodes of selection sum respectively to the total selection differential and the total selection gradient.

TABLE 2. Analyses of directional selection on male body size, z , for a population of bullfrogs (*Rana catesbeiana*) studied by Howard (1979).

Selection episode k	Selection differentials* S_k	Selection intensities i_k	Univariate selection gradients β_k
Sexual selection (mating success)	$S_1 = \bar{z}_1 - \bar{z} = .069$	$i_1 = .626$ 75%	$\beta_1 = 5.674$
Natural selection (fertility per mate)	$S_2 = \bar{z}_2 - \bar{z}_1 = .010$	$i_2 = .088$ 11%	$\beta_2 = .805$
Natural selection (offspring survivorship)	$S_3 = \bar{z}_3 - \bar{z}_2 = .013$	$i_3 = .120$ 14%	$\beta_3 = 1.084$
Total selection	$S = \bar{z}_3 - \bar{z} = .092$	$i = .832$ 100%	$\beta = 7.563$

* When using Arnold and Wade's (1984) expression (7) to calculate selection differentials, multiply the result by $n/(n-1)$. Expression (7) is for a parameter rather than its statistical estimate.

differential and shifted the mean male size distribution .63 standard deviations. Natural selection, acting through fertility per mate and offspring survivorship, produced only minor shifts in the mean size, accounting for only 11 to 14% of the total selection differential in each case (Fig. 1). The overwhelming impact of sexual selection in this population is also revealed by calculations of opportunities for selection. Sexual selection alone accounted for 59% of the total opportunity for selection (I_1/I) (Table 3). Note also the relative importance of the covariances between fitness at successive selection episodes, which account for 25% of the total opportunity for selection. Table 3 corrects some errors in computation and interpretation occurring in a similar table in Arnold (1983a).

Of course, these calculations estimate selection for only a single season of reproduction, not for a lifetime of reproductive episodes. Although it seems likely that the observed differences in fitness are truly size-related, with age playing a subsidiary role, only a longer term study could distinguish the two effects. A long-term study could also decide the issue of whether a single-season study overestimates the force of selection (because seasonal differences between individuals cancel out over the entire lifetime) or underestimates it (because size-related differences in fitness are exaggerated over lifetimes).

The interpretation of the calculated selective forces on male size are compli-

cated by the fact that Howard did not score any other phenotypic characters. The scoring of only a single phenotypic trait does not complicate the interpretation of selection differentials (since these are covariances between relative fitness and characters), but it does affect the calculation of selection gradients (since these are partial regressions of relative fitness on character). Thus with Howard's data we can calculate the univariate selection gradient on male size and its partitioning into parts corresponding to the three episodes of selection (Fig. 1), but we can not estimate the multivariate selection gradient that would describe the direct force of selection on size. The attendant ambiguities in interpreting the data are discussed by Arnold (1983a, 1983b).

What are the advantages of the data analysis we have outlined? Some of the advantages can be seen by comparing our conclusions with those of Howard (1979). Howard proposed a technique for tallying fitness across a succession of selection episodes. His technique is formally equivalent to our use of multiplicative fitness components. But because Howard did not have a technique that separates the effects of the separate episodes, some of his conclusions were erroneous. For example, to test the proposition that larger males have a greater hatching success, W_3 , Howard examined the statistical relationship between the number of hatchlings, $W_1W_2W_3$, and male body size, z , (Howard, 1979 Fig. 1). This relationship confounds selection exerted through

TABLE 3. Partitioning of the total opportunity for selection in a reproductive population of male bullfrogs (*Rana catesbeiana*) studied by Howard (1979).

Source of variance in relative fitness	Contribution to total opportunity for selection		
	Symbol	Value	Percentage
Sexual selection (mating success, w_1)	I_1	1.3822	59%
Natural selection (eggs per mate, w_2)	I_2	.2129	9%
Covariance between number of mates (w_1) and male fertility (w_2):			
Unweighted	$COI(1,2)$.5079	22%
Weighted by number of mates	$COI(1,2 1)$.0809	3%
Change in covariance between number of eggs ($w_1 w_2$) and male fertility (w_2) caused by sexual selection	$COI(12,2 1) - COI(12,2)$	-.1958	-8%
Variance in number of eggs ($w_1 w_2$)	Subtotal: I_{12}	1.9881	85%
Natural selection (hatching success, w_3)	I_3	.1599	7%
Covariance between number of eggs ($w_1 w_2$) and hatching success (w_3):			
Unweighted	$COI(12,3)$.5218	22%
Weighted by number of eggs	$COI(12,3 2)$.0315	1%
Change in covariance between number of tadpoles ($w_1 w_2 w_3$) and hatching success (w_3) caused by fertility selection	$COI(123,3 2) - COI(123,3)$	-.3640	-16%
Total selection (number of tadpoles, $w_1 w_2 w_3$)	I	2.3373	100%

hatchling survivorship with sexual and fecundity selection. The proper test of the proposition of male size-dependent survivorship of hatchlings is to examine the relationship between hatchling survivorship, W_3 , and male size (Fig. 1, third panel from top). Our analysis shows that there is no significant relationship: a result that conflicts with Howard's conclusions. Secondly, Howard used coefficients of variation (standard deviations of fitness divided by mean fitness) to measure variation in fitness. But standard deviations, unlike variances, are not additive (Fisher, 1918). By using variances in fitness, rather than coefficients of variation, we can partition the opportunity for selection into additive parts.

An Example of Data Analysis with Longitudinal Data and Two Components of Fitness.—Trivers (1976) conducted a four-year field study of social behavior and reproduction in the lizard *Anolis garmani*. Although few individuals were followed over their entire life-

times, the study does provide data on survivorship and copulatory success over a major portion of the lifetime for a relatively large sample. In our re-analysis of Trivers' data we will recognize two components of fitness: survivorship or viability, W_1 , and copulatory success, W_2 , which is the number of copulations.

Trivers did not report both viability and copulatory success for each individual. As a consequence we will not be able to partition a total selection differential nor can we calculate the covariances between viability and copulatory success. The only available course is to calculate the selection opportunities and differences separately for each fitness component, realizing the measures calculated for copulatory success may confound viability with copulatory success per se. Second, although Trivers stayed within a generation in tallying fitness, he did not actually observe the fitness component pertaining to the transition from copulation to zygote. This is probably not a

TABLE 4. Viability selection in a population of 326 male and 333 female Jamaican lizards (*Anolis garmani*) studied by Trivers (1976).

Male body size, midclass value (mm) z	Number in class $N(z)$	Survivorship per class, $\bar{W}_1(z)$	Variance within class in sur- vivorship, $\sigma^2_{w(z)}$	Class frequencies	
				$p(z)$	$p_1(z)$
55.0	27	.2963	.2085	.0828	.0540
75.0	36	.2778	.2006	.1104	.0676
85.0	56	.4286	.2449	.1718	.1622
95.0	44	.4546	.2479	.1350	.1352
105.0	39	.5128	.2478	.1196	.1351
115.0	64	.5313	.2490	.1963	.2297
≥ 125.0	60	.5333	.2489	.1841	.2163
$\bar{z} = 98.405$ $P = 438.776$	$\Sigma = 326$	$\bar{W}_1 = .4540$	$\bar{\sigma}_w^2 = .2393$	$\Sigma = 1.0000$	$\Sigma = 1.0001$

$\bar{z}_1 = 102.310, S = \bar{z}_1 - \bar{z} = 3.905 \text{ mm}, i = S/P^{1/2} = .186, V_W = \bar{\sigma}_w^2 + \sigma_b^2 = .248, V_W/\bar{W}_1^2 = 1.201$

Female body size, midclass value (mm) z	Number in class $N(z)$	Survivorship per class, $\bar{W}_1(z)$	Variance within class in sur- vivorship, $\sigma^2_{w(z)}$	Class frequencies	
				$p(z)$	$p_1(z)$
50.0	33	.2121	.1671	.0991	.0507
65.0	27	.2963	.2085	.0811	.0580
75.0	117	.4359	.2459	.3514	.3696
85.0	113	.4779	.2495	.3393	.3913
95.0	43	.4186	.2434	.1291	.1304
$\bar{z} = 77.688$ $P = 148.214$	$\Sigma = 333$	$\bar{W}_1 = .4144$	$\bar{\sigma}_w^2 = .2360$	$\Sigma = 1.0000$	$\Sigma = 1.0000$

$\bar{z}_1 = 79.67, S = \bar{z}_1 - \bar{z} = 1.986 \text{ mm}, i = S/P^{1/2} = .163, V_W = \bar{\sigma}_w^2 + \sigma_b^2 = .243, V_W/\bar{W}_1^2 = 1.413$

serious problem. In a related lizard (*A. carolinensis*) the female copulates just once for each egg that she ovulates (Crews, 1979). Third, the measurement of selection on size is complicated by age-structure in the population. As Trivers points out, larger lizards may be older or they may have grown faster. Trivers argues that copulatory success is affected by size per se, rather than by age, by showing that copulating and non-copulating lizards had similar growth rates. A more rigorous approach would have been to measure selection on hatching size and growth rate using selection gradients. This route is closed to us because size at some standard age and its correlations with growth rate and territory size were not reported. Thus we calculate selection differentials on the size at initial capture, realizing that size is confounded with age, as in Howard's bullfrog data.

The survivorships of the male and female size classes shown in Table 4 were

tabulated from Tables 14 and 15 of Trivers (1976). From these data we calculate the opportunity for viability selection and the viability selection differentials for body size in each sex (Table 4). We use the midclass values of the size classes constructed by Trivers in our estimates of selection differentials. This introduces some error into our calculation owing to the variance in size within size classes. Likewise the copulatory successes of male and female size classes shown in Tables 5 and 6 were tabulated from Table 2 of Trivers (1976). These data were used to calculate the opportunities for sexual selection and the sexual selection differentials for body size (Tables 5 and 6).

The *Anolis* data provide instructive examples of sexual differences in selection and illustrate the distinction between selection opportunities and differentials. Thus, the directional force of viability selection on males was twice the comparable force on females, even though

TABLE 5. Copulatory success in a population of 523 male Jamaican lizards (*Anolis garmani*) studied by Trivers (1976).

Male body size, midclass value (mm)	Number in class $N(z)$	Number of copulations per male, $W_2(z)$	Variance within class in copu- latory success σ_w^2	Class frequencies	
				$p(z)$	$p_2(z)$
87.5	49	.0204	.0200	.0937	.0124
92.5	46	.0652	.0610	.0880	.0370
97.5	48	.0417	.0399	.0918	.0247
102.5	40	.0000	.0000	.0765	.0000
107.5	43	.1163	.1028	.0822	.0617
112.5	40	.1750	.1444	.0765	.0864
117.5	73	.2055	.1633	.1396	.1852
122.5	88	.2046	.1627	.1683	.2222
127.5	59	.3051	.2120	.1128	.2222
132.5	37	.3243	.2191	.0708	.1482
$\bar{z} = 111.33$	$\Sigma = 523$	$\bar{W}_2 = .1549$	$\bar{\sigma}_w^2 = .1200$	$\Sigma = 1.0002$	$\Sigma = 1.0000$
$P = 197.541$					

$$\bar{z}_2 = 120.22, S = \bar{z}_2 - \bar{z} = 8.89 \text{ mm}, i = S/P^{1/2} = .63, V_W = \bar{\sigma}_w^2 + \sigma_b^2 = .1309, V_W/\bar{W}_2^2 = 5.457$$

Note: The total variance in copulatory success, V_W , is equal to the average within class variance, $\bar{\sigma}_w^2 = \Sigma p(z)\sigma_w^2 = W_2(z)[1 - W_2(z)]^2 + [1 - W_2(z)][0 - W_2(z)]^2$, plus the between class variance in copulatory success, $\sigma_b^2 = \Sigma p(z)[W_2(z) - \bar{W}_2]^2$.

there was little sexual difference in opportunity for viability selection. Thus, viability selection produced a 3.9 mm shift in mean male size but only a 2 mm shift in female size. The analysis of sexual selection revealed an even more dramatic contrast between selection differentials and opportunities. Even though the opportunity for sexual selection in females ($I = 9.9$) was nearly twice that of the males. ($I = 5.5$), the effects of sexual selection on body size were much greater in males ($S = 8.9$ mm) than in females ($S = 1.7$ mm).

An Example of Cross-Sectional Data Analysis with One Episode of Selection.—McCauley and Wade (1978) conducted a three-week study of mating behavior in the soldier beetle, *Chauliognathus pennsylvanicus*. They recorded the copulatory status (mating or non-mating) and body size (dry weight) of each beetle in their sample.

As in the previous examples, we begin by reviewing the limitations imposed by the data. First, because the data are cross-sectional rather than longitudinal they should be construed as characteristic of only the brief sample period. In order to extrapolate the selection measurements to the whole mating season, we would

have to assume that the size-dependent aspect of mating success does not vary during the season (in the case of the selection differential) and that the proportions of mating and nonmating beetles are characteristic of the whole season (in the case of the selection opportunities). Second, only a single episode of selection was measured. Thus we can measure only a portion of lifetime selection on size and of the total lifetime opportunity for selection. Furthermore, only copulatory success was scored, not mating success (the number of mates that bear progeny). Consequently we can calculate only a portion of the total opportunity or force of sexual selection. In order to calculate the total force of sexual selection we would have to know, for each individual, the fraction of copulations that result in progeny. Finally, only a single phenotypic trait was scored, body size. Consequently we cannot calculate selection gradients for size, which would represent the direct force of sexual selection on size. As always, the selection differential for size may include indirect effects of selection acting on unmeasured phenotypic correlates of size.

The body sizes of copulatory classes are tabulated in Table 6 using the data

TABLE 6. Copulatory success in a population of 651 female Jamaican lizards (*Anolis garmani*) studied by Trivers (1976).

Female body size, midclass value (mm) z	Number in class $N(z)$	Number of copulations per female $W_2(z)$	Variance within class in cop- ulatory success $\sigma_w^2(z)$	Class frequencies	
				$p(z)$	$p_2(z)$
72.5	66	.0758	.0700	.1014	.0833
77.5	101	.0693	.0645	.1552	.1167
82.5	150	.0733	.0680	.2304	.1833
87.5	166	.0843	.0772	.2550	.2333
92.5	109	.1468	.1252	.1674	.2667
97.5	59	.1186	.1046	.0906	.1167
$\bar{z} = 85.02$	$\Sigma = 651$	$\bar{W}_2 = .0922$	$\bar{\sigma}_w^2 = .0829$	$\Sigma = 1.0000$	$\Sigma = 1.0000$
$P = 51.181$					
$\bar{z}_2 = 86.67, S = \bar{z}_2 - \bar{z} = 1.65 \text{ mm}, i = S/P^{1/2} = .23, V_{W_2} = \bar{\sigma}_w^2 + \sigma_b^2 = .0837, V_{W_2/\bar{W}_2} = 9.850$					

in Table 1 of McCauley and Wade (1978) and their estimate that the frequency of mating pairs was between 5 and 10% of all observed beetles. We define the absolute fitness of copulating beetles as one and the absolute fitness of non-copulating beetles as zero. From the resulting tabulations we can calculate the selection differentials and opportunities for each sex (Table 7).

The opportunity of selection is necessarily the same for each sex ($I = 9.0$), because the estimated proportion of mating individuals is the same in both sexes.

Selection intensities (selection differentials divided by phenotypic standard deviations before selection) are useful for comparing selective pressures in different populations (Falconer, 1981). They measure the shift in mean caused by directional selection in units of phenotypic standard deviation. For example, the force of sexual selection on male body size was very similar in Howard's bullfrog and in Trivers' lizard population. In both cases larger males had greater mating success and sexual selection on body size is almost three times greater in males than in females in the lizard population (Tables 5 and 6). In contrast, in the beetle population studied by McCauley and Wade (1978), sexual selection caused only a minor shift in mean male size, .15 standard deviation. Indeed, the intensity of sexual selection on size was comparable in males and females (Table 7).

DISCUSSION

Selection analysis can be viewed as a four-stage process in which progress is constrained by both the kind and amount of data. (1) If we have data on individual fitness, we can estimate a selection opportunity and place an upper limit on the intensity of selection that can act on any one character. (2) If we also have measurements of some phenotypic character, we can estimate a selection differential that describes the direct and indirect forces of directional selection on that character. (3) If we measure a whole suite of characters we can estimate the selection gradients that describe the direct forces of selection on each character. (4) Finally, if we accomplish multivariate phenotypic measurements in a very large sample, we can estimate stabilizing selection gradients that describe the direct forces of stabilizing (and disruptive) selection on the characters. These gradients can also be used to reconstruct a multi-dimensional selection surface (Lande and Arnold, 1983). A number of contemporary studies in natural populations have succeeded at the difficult first stage of measuring fitness and a few have proceeded to the second or third stage. We do not know of any published studies that do a thorough job at the fourth stage.

Estimates of fitness variance in nature have revealed large opportunities for selection (Wade and Arnold, 1980; Clut-

ton-Brock, 1983; McCauley, 1983). Most studies have concentrated on variance in progeny number in a single reproductive season. For example, Kluge (1981) has compiled and analyzed data from a large number of anuran studies. In males, the average opportunity for selection (variance in relative egg count) was 2.8 (range .5–5.9) in a sample of 13 species, but some species showed tremendous year-to-year variation. This average opportunity, if focused on a single trait, could shift the mean by nearly 1.7 standard deviations. Under a model of truncation selection on a normally distributed trait, this selection intensity is equivalent to selecting the upper 12% of males. In nearly all species over 90% of the selection opportunity was due to sexual selection. Our analysis of Howard's bullfrog data gave results in line with Kluge's. Variance among males in hatching success provided some additional opportunity for selection in bullfrogs, but sexual selection accounted for most of the total.

The means of phenotypic characters can shift appreciably during brief episodes of selection. Unfortunately, most workers have merely tested for the presence of directional selection and have not estimated its magnitude. In the data we analyzed, sexual selection on males shifted mean body size by nearly two-thirds of a standard deviation in populations of bullfrogs and *Anolis* lizards (in both cases size was confounded with age) and by .15 standard deviations in a cohort of soldier beetles. Natural selection exerted by severe weather can produce comparable intensities of directional selection. A drought on the Galápagos Islands favored larger finches (*Geospiza fortis*), shifting mean body size by .71 standard deviations (Boag and Grant, 1981). A winter storm favored smaller house sparrows (*Passer domesticus*), shifting the average body weight in the sample by about a quarter of a standard deviation (Bumpus, 1899; Lande and Arnold, 1983).

Many additional instances of selection can be gleaned from the literature (Johnson, 1976; Berry, 1977). Nevertheless, the

TABLE 7. Copulatory success in a population of soldier beetles (*Chauliognathus pennsylvanicus*) studied by McCauley and Wade (1978).

Average male body size, dry weight (g), z	Copulatory status* $W(z)$	Class frequency $p(z)$
.01430	1	.10
.01382	0	.90
$\bar{z} = .01387$	$\bar{W} = .10$	1.00
$P = .000008$		
$\bar{z}_1 = .01430, S = \bar{z}_1 - \bar{z} = .00043,$ $i = S/P^{1/2} = .1520,$ $V_W = .09, V_W/\bar{W}^2 = 9.0$		
Average female body size, dry weight (g), z	Copulatory status* $W(z)$	Class frequency $p(z)$
.01826	1	.10
.01720	0	.90
$\bar{z} = .01731$	$\bar{W} = .10$	1.00
$P = .000019$		
$\bar{z}_1 = .01826, S = \bar{z}_1 - \bar{z} = .000095,$ $i = S/P^{1/2} = .2180,$ $V_W = .09, V_W/\bar{W}^2 = 9.0$		

Note: Average copulatory success is equal to the frequency of the mating class, $\bar{W} = p(1)(1) + [1 - p(1)](0) = p(1) = .10$.

* The copulatory status of mating beetles is one and the copulatory status of the nonmating beetles is zero.

examples reviewed here are representative of the sophistication that has been achieved in field studies. Additional progress could be made in a number of ways: (1) by measuring lifetime fitness, as well as its components, (2) by scoring a number of characters and (3) by combining studies of selection and inheritance.

Lifetime fitness has been measured in a surprisingly small number of field studies (Clutton-Brock et al., 1982; Clutton-Brock, 1983). Measurement of lifetime fitness is a prerequisite for characterization of the effects of lifetime selection on phenotypic characters, for a complete comparison of how selection acts on the sexes and for numerous other problems. Perhaps the most speedy progress will be made with annual plants and short-lived arthropods. Simulations of lifetime fitness based on data from only part of the life cycle (Howard, 1983) are unlikely to provide a completely satisfactory substitute for direct measurement. One obsta-

cle to using simulations is the complexity of correlations between fitness components (Arnold and Wade, 1984). These correlations cannot be calculated from incomplete data. On the other hand, many important questions do not require data on lifetime fitness and depend instead on accurate tallies of fitness during parts of the life cycle. To contrast sexual selection in males and females, for example, we only need data on mating success and can ignore previous events in the life cycle.

Most studies of selection have focused on a single character. In studies of sexual selection, for example, investigators score body size and tend to ignore other characters. Single-trait myopia can give a misleading picture of selection. Selection may actually have acted on correlated characters rather than on the character in focus (Lande and Arnold, 1983).

Only a few investigators have succeeded in measuring both selection on polygenic characters and their patterns of inheritance. Even the first few studies of this kind have yielded some surprises. McGregor et al. (1981) documented lifetime stabilizing selection on the song repertoire size of great tits (*Parus major*) but this trait showed no demonstrable heritable variation. Boag (1983) showed that numerous body dimensions of Galápagos finches (*Geospiza fortis*) were heritable and genetically correlated. Consequently, the strong directional selection on body size in these birds documented by Boag and Grant (1981) had complex morphological ramifications due to the genetic coupling of characters. Lande (1979) shows how studies of selection and quantitative inheritance can be combined to model multivariate evolution.

SUMMARY

The study of selection in natural populations is a neglected field. So far only a few investigators have succeeded in measuring lifetime fitness or selection on multiple phenotypic characters. Studies of multiple selection episodes are also rare. Most traits of interest to ecologists

and evolutionists are polygenic with complex patterns of genetic coupling (Wright, 1978), but only a few field workers have combined studies of selection and inheritance. Consequently we do not yet have a clear view of multivariate selection in nature or its evolutionary consequences.

In this paper we apply statistical measures of selection discussed in the companion paper (Arnold and Wade, 1984) to the analysis of multiple selection episodes. The advantage of the measures we use is that they are directly related to coefficients of selection used in theoretical equations for evolutionary change. We analyze selection exerted during particular segments of the life cycle by dividing total fitness into multiplicative components (e.g., viability, fecundity, fertility). Selection on a phenotypic trait during a particular part of the life cycle can then be measured by the statistical relationship between the corresponding fitness component and the trait. Furthermore, the portions of selection corresponding to particular fitness components or selection episodes will sum to the total selection acting on the trait. This additive property of the selection measures depends on a multiplicative definition of fitness components and has several uses.

Our partitioning of selective force has three principal uses. First, it allows a characterization of selection when it is possible to measure portions of fitness but impractical to record total, lifetime fitness. A particularly useful property is that one obtains the same estimate of selection during an episode using complete or incomplete data on lifetime fitness. Second, even when total fitness can be measured, it will often be desirable to measure the forces exerted by separate episodes of selection, since selection may change in magnitude and direction during different stages of life. For example, in a re-analysis of Howard's (1979) data on the fitness of male bullfrogs during a single reproductive season, we found that sexual selection accounted for most of

the selection on body size with only minor contributions from two forms of natural selection. Finally, partitioning of selective forces may help identify the actual agents of selection. Thus a demonstration that selection acts during a particular short segment of the life cycle can narrow the field of candidate selective agents. For example, we briefly discuss some examples of strong directional selection arising from severe weather conditions.

ACKNOWLEDGMENTS

This work was supported by PHS grants 1-K04-HD-00431 (to MJW) and 1-K04-HD-00392-01 (to SJA), and NIH grant GM-22523 (to MJW), and NSF grants NSF BNS 80-14151 and NSF DEB 81-11489 (to SJA) and NSF DEB 82-00347 (to MJW). We are grateful to James Cheverud, T. H. Clutton-Brock, James Crow, R. D. Howard, Russell Lande, David McCauley, Craige Pease and an anonymous reviewer for discussion and comments on the manuscripts of this paper and its companion, Arnold and Wade (1984). The manuscripts were greatly improved by the detailed and helpful criticism offered by Michael Bulmer.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-267.
- ARNOLD, S. J. 1983a. Sexual selection: the interface of theory and empiricism, p. 67-107. *In* P. G. Bateson (ed.), *Mate Choice*. Cambridge Univ. Press.
- . 1983b. Morphology, performance and fitness. *Amer. Zool.* 23:347-361.
- ARNOLD, S. J., AND L. HOUCK. 1982. Courtship pheromones: evolution by natural and sexual selection, p. 173-211. *In* M. Nitecki (ed.), *Biochemical Aspects of Evolutionary Biology*. Univ. Chicago Press, Chicago.
- ARNOLD, S. J., AND M. J. WADE. 1984. On the measurement of natural and sexual selection: theory. *Evolution* 38:709-719.
- ATCHLEY, W. R., AND J. J. RUTLEDGE. 1981. Genetic components of size and shape I. Dynamic components of phenotypic variability and covariability during ontogeny in the laboratory rat. *Evolution* 35:1161-1173.
- BERRY, R. J. 1977. *Inheritance and Natural History*. Collins, London.
- BOAG, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galápagos. *Evolution* 37:877-894.
- BOAG, P. T., AND P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (*Geospizinae*) in the Galapagos. *Science* 214:82-84.
- BROWNLEE, K. A. 1965. *Statistical Theory and Methodology in Science and Engineering*. John Wiley and Sons, Inc., N.Y.
- BUMPUS, H. C. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Biol. Lecture. Woods Hole Marine Biol. Stat.* 6:209-226.
- CHARLESWORTH, B. 1980. *Evolution in Age-structured Populations*. Cambridge Univ. Press, Oxford.
- CLUTTON-BROCK, T. H. 1983. Selection in relation to sex, p. 457-481. *In* D. S. Bendall (ed.), *Evolution From Molecules to Man*. Cambridge Univ. Press.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Univ. Chicago Press, Chicago.
- COCK, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quart. Rev. Biol.* 41:131-190.
- CREWS, P. 1979. Neuroendocrinology of lizard reproduction. *Biol. Reprod.* 20:51-73.
- CROW, J. F., AND M. KIMURA. 1970. *Introduction to Population Genetics Theory*. Harper and Row, N.Y.
- DARWIN, C. 1859. *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- . 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- FISHER, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. Roy. Soc. Edinburgh* 52:399-433.
- GHISELIN, M. T. 1974. *The Economy of Nature and the Evolution of Sex*. Univ. Calif. Press, Berkeley.
- HOWARD, R. D. 1979. Estimating reproductive success in natural populations. *Amer. Natur.* 114:221-231.
- . 1983. Sexual selection and variation in reproductive success in a long-lived organism. *Amer. Natur.* 122:301-325.
- JOHNSON, C. 1976. *Introduction to Natural Selection*. Univ. Park Press, Baltimore.
- KLUGE, A. G. 1981. The life history, social organization and parental behavior of *Hyla rosenbergi* Boulenger, a nest building gladiator frog. *Misc. Publ. Mus. Zool. Univ. Michigan* no. 160: 1-170.
- LANDE, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402-416.
- . 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:294-305.

- . 1982. A quantitative genetic theory of life history evolution. *Ecology* 62:607–615.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- MCCAULEY, D. E. 1983. An estimate of the relative opportunities for natural and sexual selection in a population of milkweed beetles. *Evolution* 37:701–707.
- MCCAULEY, D. E., AND M. J. WADE. 1978. Female choice and the mating structure of a natural population of the soldier beetle, *Chauliognathus pennsylvanicus*. *Evolution* 32:771–775.
- MCGREGOR, P. K., J. R. KREBS, AND C. M. PERRINS. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *Amer. Natur.* 118:149–159.
- PRIMACK, R. B., AND J. ANTONOVICS. 1981. Experimental ecological genetics in *Plantago*. V. Components of seed yield in the ribwort plantain, *Plantago lanceolata* L. *Evolution* 35:1069–1079.
- PROUT, T. 1965. The estimation of fitness from genotypic frequencies. *Evolution* 19:546–551.
- TRIVERS, R. L. 1976. Sexual selection and resource-accurring abilities in *Anolis garmani*. *Evolution* 30:253–269.
- WADE, M. J. 1979. Sexual selection and variance in reproductive success. *Amer. Natur.* 114:742–747.
- WADE, M. J., AND S. J. ARNOLD. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. *Anim. Behav.* 28:446–461.
- WRIGHT, S. 1968. *Evolution and the Genetics of Populations, Vol. I. Genetic and Biometric Foundations*. Univ. Chicago Press, Chicago.
- . 1978. *Evolution and the Genetics of Populations, Vol. IV. Variability Within and Among Populations*. Univ. Chicago Press, Chicago.

Corresponding Editor: J. Felsenstein