

A comparison of methods to partition selection acting via components of fitness: Do larger male bullfrogs have greater hatching success?

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Abstract

We contrast three methods for measuring selection at sequential fitness components (here called the additive, changing variance, and independent methods). The independent method (Koenig and Albano, 1987; Conner, 1988) describes the relationship between a phenotypic character and one fitness component independent of other components. This method is appropriate when the question is whether or not a character has fitness consequences independent of selection at other stages. The additive (Arnold and Wade, 1984a) and changing variance (Kalisz, 1986; Koenig and Albano, 1987) methods measure selection via one component of fitness, taking into consideration constraints imposed by selection via earlier components in the sequence. These methods therefore more accurately track selection over a sequence of fitness components. Of these latter two methods, the changing variance method yields erratic results in simulation studies and is not recommended in its unmodified form. The additive method (equivalent to the changing variance method weighted as described in Wade and Kalisz [1989]) explicitly partitions selection into additive components and is useful for measuring selection taking into account the constraints imposed by selection acting via prior fitness components.

The methods often yield very different estimates of the relative degree to which the mean of a character is changed by selection acting via a particular component of fitness (the “strength” of selection). However, neither the additive nor independent method is inherently superior to the other; rather, these measures are complementary.

Powerful techniques have recently been developed for quantifying selection (Lande and Arnold, 1983; Manly, 1985; Schluter, 1988; Crespi and Bookstein, 1989). A method of partitioning directional selection, derived by Arnold and Wade

(1984a), is of particular interest to population biologists because it describes how selection acts via different components of fitness, also referred to as episodes of selection. This method allows researchers to use longitudinal data to identify which components of fitness are most important with respect to selection. Components of fitness are ordered and multiply to equal the total fitness measured. For example, lifespan (days alive), mating efficiency (mates/day) and success in fertilizing eggs (fertilizations/mate) multiply to equal the total number of fertilizations a male obtains during his lifetime. The number of fitness components examined is flexible and depends on the both the biology of the species and the data acquired by the researcher.

In addition to the method described by Arnold and Wade (1984a), two alternative procedures for measuring selection at sequential fitness components have been used in recent studies (Kalisz, 1986; Koenig and Albano, 1987; Conner, 1988). Here we compare the three methods and illustrate their differences with the goal of understanding how the values derived illuminate how selection works. Our results suggest that the method of choice will depend in part on the goal of the analysis and on whether one desires (1) a picture of selection constrained by changes in phenotypic variation or (2) to focus on the relationship between a character and a particular component of fitness.

Because Arnold and Wade's (1984a) method partitions selection that modifies the mean of a character, we restrict our discussion to directional selection and ignore stabilizing or disruptive selection, which modifies the variance in a character independent of the mean (Lande and Arnold 1983). We also do not discuss more recent techniques, such as the cubic-spline method of Schluter (1988), to visualize the form of selection. This alternative technique is useful for examining selection at particular stages but has not as yet been extended to sequential components of fitness.

First we briefly discuss derivation of the methods. We then compare them using data from Howard's (1979) classic study of male bullfrogs (*Rana catesbeiana*) and simulations based on several hypothetical data sets.

Definitions and methods

The selection differential, s , measures the shift in the mean of a character due to selection (Falconer, 1981). Selection differentials divided by character variance (P) yield selection gradients (β), which measure the relative strength of selection (Lande, 1979; Lande and Arnold, 1983). Selection differentials are equal to the covariance between relative fitness (w) and the phenotypic character (z) under consideration (Robertson, 1966).

When fitness is divided into multiplicative components, the selection differential can be partitioned into components, s_k (Arnold and Wade, 1984a). Values of s_k measure the shift in the mean of a character due to selection acting via the k th component of fitness and are equal to the mean of the character after the action of all components up through component k minus the mean before component k .

When defined according to the equations given in Arnold and Wade (1984a, p. 712), s_k values are equal to the covariance between phenotypic value and the k th component of relative fitness. That is,

$$s_k = \text{COV}(z, w_k). \quad (1)$$

All individuals are included in the calculations for each component, and consequently s_k values are additive and sum to the total selection differential, S . Complete derivation of s_k values is provided by Arnold and Wade (1984a).

There are two types of selection differentials that can be calculated using s_k values. First is β_k , equal to the additive selection differential (s_k) at episode k divided by the variance in the original distribution of the trait (P_0), multiplied by $N/[N - 1]$. (For clarity, we ignore the $N/[N - 1]$ term in the subsequent discussion.) That is,

$$\beta_k = s_k / P_0. \quad (2)$$

In the multivariate case, $\beta_k = \mathbf{P}^{-1} \mathbf{S}_k$, where \mathbf{P}^{-1} is the inverse of the phenotypic variance-covariance matrix before selection, \mathbf{S}_k is the column vector of selection differentials at episode k , and β_k is the column vector of selection gradients at episode k . The multivariate technique separates selection acting directly on a character from selection acting indirectly through measured correlated characters (Lande and Arnold, 1983).

As with s_k , β_k values are additive and sum to β_{Total} , the total selection differential over m episodes. Hence, we refer to this derivation for selection gradients as the "additive" method.

The second selection gradient that can be calculated from s_k values was mentioned but not emphasized by Arnold and Wade (1984a). We call this selection gradient β_k^* , defined as the selection differential at the k th episode (s_k) divided by the variance in the character at the *onset* of episode k rather than the original variance in the character, P_0 . That is,

$$\beta_k^* = s_k / P_{k-1}. \quad (3)$$

For the first episode, $P_{k-1} = P_0$ and $\beta_k^* = \beta_k$. However, for subsequent episodes, $\beta_k^* \neq \beta_k$, except for the unlikely case in which $P_{k-1} = P_0$. In the multivariate case, $\beta_k^* = \mathbf{P}_{k-1}^{-1} \mathbf{S}_k$, where \mathbf{P}_{k-1}^{-1} is the inverse of the phenotypic variance-covariance matrix before episode k (that is, weighted by cumulative fitness at episode $k - 1$) and β_k^* is the column vector of selection gradients at episode k . (Arnold and Wade [1984a, p. 712] defined β_k^* values using \mathbf{P}_k . We have used \mathbf{P}_{k-1} because all other subscripts, k , both in their paper and here, refer to parameters up through rather than prior to episode k .)

Because the fitness components multiply to lifetime fitness (by definition) and the character variance changes at each episode, β_k^* values are not additive and do not sum to β_{Total} . β_k^* values are, however, readily converted to additive β_k values by the weighting factor $\mathbf{a}_k = \mathbf{P}_0^{-1} \mathbf{P}_{k-1}$ (Wade and Kalisz, 1989). We refer to β_k^* as the "changing variance" method of measuring selection gradients via sequential fitness components.

An alternative to using s_k values to derive selection gradients is to define selection differentials as the shift in the mean of the character using only individuals effectively contributing to component k (Koenig and Albano, 1987; Conner, 1988). To calculate s'_k , we define relative fitness for individual j at component k , $w'_{k,j}$, explicitly excluding individuals whose fitness at a prior component is zero. That is,

$$w'_{k,j} = W_{k,j} / \left(\sum W_{k,j} / N' \right), \quad (4)$$

where $W_{k,j}$ is absolute fitness during episode k and N' is the number of individuals for which $W_{k-1} > 0$. We then define s'_k as the covariance between relative fitness, w'_k , and the character,

$$s'_k = \text{Cov}(z, w'_k). \quad (5)$$

Note that this equation is identical to equation (1), above, except that individuals whose fitness at a prior episode is zero are excluded from the calculations. Values of s'_k do not sum to S because the reference population shifts following each episode as individuals with zero fitness for a given fitness component drop out of the calculations.

Using s'_k , a third selection gradient, β'_k , can be derived by dividing s'_k by the variance in the character among individuals for which $W_{k-1} > 0$. Hence,

$$\beta'_k = s'_k / P'_{k-1}, \quad (6)$$

where P'_{k-1} is the variance in the character using only individuals whose fitness is greater than zero at the onset of component k (that is, $W_{k-1} > 0$). In the multivariate case, $\beta'_k = \mathbf{P}'_{k-1}{}^{-1} \mathbf{S}'_k$, where $\mathbf{P}'_{k-1}{}^{-1}$ is the inverse of the phenotypic variance-covariance matrix including only individuals whose fitness is greater than zero at the onset of component k , β'_k is the column vector of selection gradients, and \mathbf{S}'_k is the column vector of selection differentials at component k . Analogous to s'_k , each element in the \mathbf{S}'_k matrix is the covariance between the character value and relative fitness defined by the ratio $W'_{k,j} / (\sum W_{k,j} / N')$, and thus includes only those individuals for which $W_{k-1} > 0$.

β'_k can also be derived directly by regression of relative fitness at each episode (w'_k as defined in equation [4]) on the character. Therefore β'_k is a true regression coefficient (Conner, 1988). However, the reference population explicitly changes at each episode because individuals with $W_{k-1} = 0$ drop out of the calculations. Values of β'_k , like those of β^*_k , are not additive and do not sum to β_{Total} when components multiply to lifetime fitness. We refer to this as the "independent" method of partitioning selection gradients because β'_k is not influenced by performance at other episodes other than by elimination of individuals whose fitness is zero.

There are two noteworthy situations in which the various measures of selection discussed above are equivalent. First, because all individuals start with equal fitness in the first episode, $s'_1 = s_1$, $P'_0 = P_0$, and consequently $\beta'_1 = \beta^*_1 = \beta_1$. These equalities do not hold in general for $k > 1$. However, $s'_k = s_k$ for all k when fitness at each component is an all or none affair, that is, either $W_k = 1$ or $W_k = 0$. Similarly, when

$W_k = 1$ or $W_k = 0$, the weighted phenotypic variance prior to component k , P_{k-1} , equals P'_{k-1} , the phenotypic variance for individuals with $W_{k-1} > 0$. It follows that $\beta_k^* = \beta'_k$ when $W_k = 1$ or $W_k = 0$. Proof is beyond the scope of this paper, but can be confirmed by performing analyses using components which take on only these two values. An example of such data is provided by Kalisz (1986), whose episodes each represented survivorship to the next life-history stage. However, since such data are categorical rather than continuous, the appropriateness of using a regression model to analyze them is questionable (Sokal and Rohlf, 1981, p. 454).

Statistical testing of measures of selection can be accomplished by use of Wu's (1986) weighted jackknife estimator (Mitchell-Olds and Shaw, 1987). A computer program, written in Fortran, which calculates the three types of selection gradients and their confidence intervals for up to four characters and seven episodes of selection, is available from the authors on request.

Results

Selection on Male Bullfrogs

Howard's (1979) data on the relationship between size and fitness of male bullfrogs provide a useful comparison of the methods for calculating selection gradients. Howard measured fitness at three stages in the life cycle: number of mates, number of zygotes, and number of hatchlings. Episode 1 is number of mates, episode 2 is the number of zygotes per mate (fertility per mate), and episode 3 is hatchlings per zygote (hatching success of offspring survivorship). Multiplying these three components together yields the total number of hatchlings. The episodes cross generational boundaries, and therefore are not ideal insofar as selection may be confounded with inheritance. However, the episodes can be analyzed by the methods discussed here because they are sequential and multiplicative.

Based on correlations with male body size, Howard (1979) concluded that larger males experience greater mating success, fertilize more eggs, and produce more hatchlings. Arnold and Wade (1984b) reanalyzed Howard's data and concluded, based on the additive method, that the majority of selection in male bullfrogs occurred via the first fitness component, mating success, and that no significant selection on male body size occurred via fertility per mate or hatching success.

Table 1 presents a reanalysis of Howard's (1979) data using the above three methods for calculating selection gradients. The additive method (β_k), supports Arnold and Wade's (1984b) conclusion that there is significant directional selection on body size only via the first fitness component, mating success. Selection acting via the second fitness component, fertility per mate, is not significant by any of the three methods. However, both the changing variance (β_k^*) and independent (β'_k) methods indicate significant directional selection on body size via the third fitness component, hatching success. Thus, whether it can be concluded that larger males have greater hatching success or not depends on the method used to partition the selection gradient.

Table 1. Selection gradients (\pm SE) for Howard's bullfrog data *

Episode (k)	Selection gradients		
	β_k	β_k^*	β'_k
1. Mating success	$5.65 \pm 1.19^{***}$	$5.65 \pm 1.19^{***}$	$5.65 \pm 1.19^{***}$
2. Fertility per mate	0.85 ± 0.67	2.64 ± 1.65	2.45 ± 1.54
3. Hatching success	1.10 ± 0.62	$4.35 \pm 1.67^*$	$4.00 \pm 1.51^*$
Total selection (β_{Total})	$7.60 \pm 1.60^{***}$	—	—

$N = 38$ individuals. Standard errors and significance values calculated using the delete-one weighted jackknife procedure (see text).

* $P < 0.05$; *** $P < 0.001$; other $P > 0.05$.

Simulation studies

In this section we examine the performance of the above methods of calculating selection gradients under several hypothetical selection regimes. First, we consider three selection regimes: (1) reinforcing directional selection, both for larger and smaller quantitative characters, (2) selection that reverses direction in successive episodes, and (3) cases in which individuals attain zero fitness at episodes prior to the last. In all examples, seven sequential fitness components are measured. The absolute fitnesses of each individual during episode k (W_k) are listed in the Appendix. Cumulative fitness after each episode is not listed, but can be calculated by multiplying the appropriate set of absolute fitness values.

Reinforcing directional selection

Consider five individuals ($n = 1$ to 5) whose character values, z are 11, 12, 13, 14, and 15 (for simplicity, we call the character body size). At each episode, let the absolute fitness of individual 1 equal 1, individual 2 equal 2, and so on (see Appendix); thus, the cumulative fitness of each individual n after episode k is n^k . Under these conditions, each individual's divided relative fitness, w_k , is identical during each episode.

As shown in Fig. 1a, β'_k values for this example are the same for all episodes, reflecting the equivalence of selection acting via each component of fitness. In contrast, β_k values decrease markedly with each episode, asymptotically approaching zero. β_k^* values are intermediate and are closer to β'_k than to β_k .

Compared to the independent method, example 1 demonstrates how s_k and β_k values are constrained by selection occurring during earlier episodes. Consequently, it is difficult to envisage even a hypothetical example in which s_k , and thus β_k , consistently increase in successive components. This is suggested by example 2, in which fitness at each episode is equal to n^k and therefore cumulative fitness is equal to $n^{\Sigma k}$, at each episode. Except for a very small increase in β_2 over β_1 , β_k still decreases markedly, while both β'_k and β_k^* increase with successive episodes (Fig. 1b).

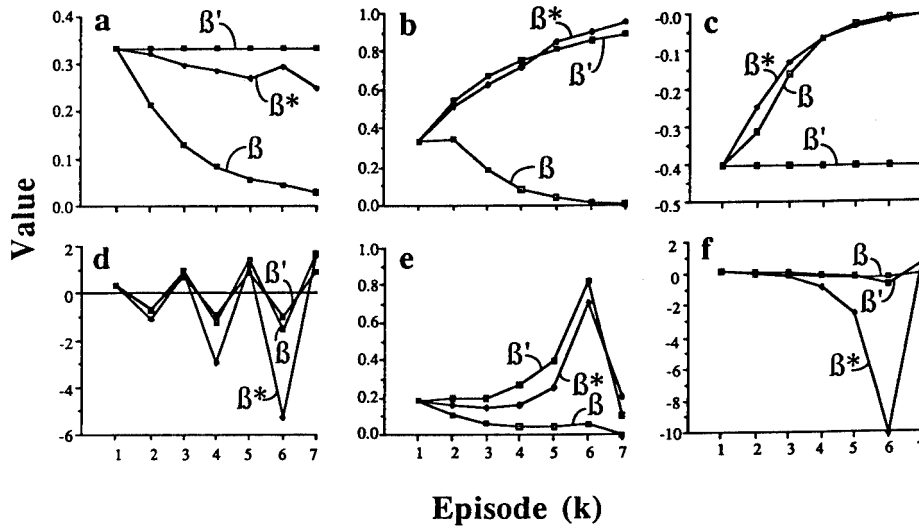


Fig. 1. — Values of β_k , β'_k , and β^*_k for the six examples described in the text: (a) reinforcing directional selection, equivalent at each episode, favoring large size, (b) reinforcing directional selection, increasing at each episode, favoring large size, (c) reinforcing directional selection, equivalent at each episode, favoring small size, (d) selection favoring large and small individuals alternately at each episode, (e) directional selection favoring large individuals reinforced by reproductive failure among the smallest individuals at early episodes, and (f) directional selection favoring large individuals countered by reproductive failure among the largest individuals at early episodes. Raw data used for these examples are listed in the Appendix.

Example 3 is the converse of example 1 in that selection favors smaller individuals by a factor of z at each episode, and cumulative fitness is n^{-k} at episode k . Again, the results show that β'_k remains constant while β_k increases asymptotically to zero (Fig. 1c). In contrast to the prior examples, β^*_k is more similar to β_k than to β'_k . However, the behavior of β^*_k seems to depend on the exact fitness values used, as other simulations of selection for smaller size yielded β^*_k similar to β'_k .

Selection reversing direction at each episode

In example 4, the direction of selection reverses and the magnitude increases with successive episodes. Specifically, for individual n , divided absolute fitness, W_k , is equal to n^k at odd and n^{-k} at even episodes such that cumulative fitness is $n^{(k+1)/2}$ at odd and $n^{-(k/2)}$ at even episodes (see Appendix). Under these conditions all three selection gradients are very similar at odd episodes when selection is for larger size (Fig. 1d). At even episodes, when selection reverses direction and favors small individuals, β_k and β'_k are alike while β^*_k is considerably more negative.

Individuals drop out of the calculations

The third category of data studied here is that in which the fitness of some individuals equals zero such that they drop out of the calculations for s'_k and β'_k .

Two examples are examined. In both, ten individuals of size 11 to 20 are subjected to a selection regime similar to that in example 1. In example 5, successively larger individuals drop out of the calculations such that failure among the smallest individuals reinforces selection for large size among the remaining sample. Example 6 is identical except that larger individuals successively drop out such that reproductive failure opposes the advantage of large size among the remaining individuals (see Appendix).

Results from analyses of these two examples are presented in Figs. 1e and 1f. In the first, β'_k and β_k^* are relatively similar. Both remain constant for several episodes and then increase until the last episode, while β_k decreases with each episode. In example 6, β_k and β'_k are similar and remain close to zero over all episodes, while β_k^* increases exponentially as individuals drop out, reaching a highly negative value at episode 6 (Fig. 1f). This is similar to the performance of the different selection gradients under the conditions of reversing selection simulated in example 4, but again appears to be dependent on the precise form of the data set.

One additional example serves to clarify the difference between β_k and β_k^* , both of which are influenced by selection occurring during earlier episodes, and β'_k , which is not. Consider six individuals, two each of sizes 11, 12, and 13. Imagine that three of them (of sizes 11, 12, and 13) survive for only one day and obtain 3, 2, and 1 matings, respectively, during that day. The other three (also of sizes 11, 12, and 13) survive for 10 days and obtain 10, 20, and 30 matings (e.g., 1, 2, and 3 matings per day), respectively, during their lives. The raw data for this example and results of the analyses are given in Table 2. Note that there is no directional selection on

Table 2. Partitioning of selection in a hypothetical population showing how weighting at a prior episode influences selection gradients

A. Data				
Individual	Size (z)	Survivorship (Days Alive, W_1)	Mating Success (Mates/Day Alive, W_2)	Total Mates ($W_1 W_2$)
1	11	1	3	3
2	12	1	2	2
3	13	1	1	1
4	11	10	1	10
5	12	10	2	20
6	13	10	3	30

B. Analysis		
Selection gradient	Component of fitness	
	Survivorship	Mating success
β_k	0.00	0.41
β_k^*	0.00	0.48
β'_k	0.00	0.00

size expressed through survivorship, since mean survivorship is equal for each size class. There is also no selection via mating success as measured by β'_2 , since selection for small size among those individuals surviving for only one day is exactly counterbalanced by selection for large size among individuals surviving for 10 days. In contrast, both β_2 and β_2^* suggest selection for large size via the second fitness component, mating success. This is because individuals with relatively lower fitness in the first episode are given proportionally less weight in calculation of β_k and β_k^* during subsequent episodes. This is not the case for β'_k .

Discussion

Each method of calculating selection gradients yields different results. In calculating s_k , β_k , and β_k^* , the character distribution on which selection acts is weighted by success at prior episodes. Although the character distribution used to calculate s_k changes from one component to the next, the reference population remains the same. In contrast, the reference population explicitly shifts between episodes when calculating s'_k and β'_k whenever any individuals die or experience reproductive failure, as in Howard's bullfrog data and examples 5 and 6, above.

Using the changing variance method, the selection gradient β_k^* is calculated using the variance in the character modified by selection acting via prior fitness components. In most of the examples considered here, directional selection decreases the variance in the character with successive episodes. When β_k^* is positive, as in Figs. 1a and 1b, the decreased variance compensates for the decline in s_k relative to s'_k and yields a β_k^* similar to β'_k . When β_k^* is negative, as in Figs. 1c and 1f, or oscillates in sign with each episode, as in Fig. 1e, the behavior of β_k^* is erratic and depends on the data. Because of its apparent unpredictability, we do not recommend its usage, and exclude this measure from further discussion. Additional discussion of the shortcomings of β_k^* are provided by Wade and Kalisz (1989), who also provide details on the conversion of β_k^* to β_k values.

We view s_k and β_k as measures of the selection realized via one fitness component, taking into account the constraints imposed by selection during prior components (see also Wade and Kalisz 1989). In contrast, s'_k and β'_k measure the relationship between a character and each fitness component independent of selection during prior fitness events. For example, in the hypothetical data analyzed in Table 2, β'_2 reflects the fact that larger males are not more efficient at obtaining matings. However, the positive β_2 values indicate that selection for larger size by increased mating success does occur as a consequence of the interaction of this episode with β_1 (survivorship).

What of Howard's bullfrog data and the question of whether male size influences hatching success? On the basis of β'_3 (Table 1), we believe it is appropriate to conclude that male size has a significantly positive influence on offspring survivorship. This result poses some potentially interesting questions: (1) Do larger males acquire better quality territories or do they defend eggs from predators? (2) Do females benefit by mating with larger males due to greater survivorship of offspring

in high quality territories? Use of the additive method fails to reveal a relationship between male body size and offspring survivorship, halting further hypothesis testing along these lines. However, the additive method more accurately depicts the importance of offspring survivorship to overall selection on body size of males. Using this method, β_3 is small and not significant because it is constrained by selection acting via the first fitness component, mating success.

The choice of which measure to use must ultimately be based on the goals of the analysis. If the goal is to determine whether there is a significant relationship between a quantitative character and some component of fitness, as will usually be the case in studies of the functional consequences of behaviors, the independent method is preferable. This method is also appropriate for any set of components that multiply to lifetime fitness even if they are not sequential, since β'_k values are independent of the order of components. However, this method is not meant to replace a rigorous experimental approach to determining the function of a behavior, but is simply a way of determining whether a predicted relationship between the behavior and fitness is manifest in nature.

Alternatively, if the goal is to track selection acting via sequential components of fitness, as will usually be the case in studies of quantitative genetics, the additive method is more appropriate. We do not believe that either one of the measures is "correct" in the sense that it is better than the other. Instead, both quantify selection from different perspectives and must be interpreted accordingly. As such, they should be viewed as complementary, rather than competing, measures of selection. DD⁰

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References

- Arnold, S. J. and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709-719.
- Arnold, S. J. and M. J. Wade. 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38: 720-734.
- Conner, J. 1988. Field measurements of natural and sexual selection in the fungus beetle, *Bolitotherus cornutus*. *Evolution* 42: 736-749.
- Crespi, B. J. and F. L. Bookstein. 1989. A path-analysis model for the measurement of selection on morphology. *Evolution* 43: 18-28.
- Falconer, D. S. 1981. *Introduction to Quantitative Genetics*, 2nd Ed. Longman, London.
- Howard, R. D. 1979. Estimating reproductive success in natural populations. *Amer. Natur.* 114: 221-231.
- Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40: 479-491.

Example d: Selection reversing direction at each episode

1	11	1	1	1	1	1	1	1
2	12	2	2^{-2}	2^3	2^{-4}	2^5	2^{-6}	2^7
3	13	3	3^{-2}	3^3	3^{-4}	3^5	3^{-6}	3^7
4	14	4	4^{-2}	4^3	4^{-4}	4^5	4^{-6}	4^7
5	15	5	5^{-2}	5^3	5^{-4}	5^5	5^{-6}	5^7

Example e: Directional selection for large size reinforced by failure among small individuals

1	11	1	0	-	-	-	-	-
2	12	2	2	0	-	-	-	-
3	13	3	3	3	0	-	-	-
4	14	4	4	4	0	-	-	-
5	15	5	5	5	5	0	-	-
6	16	6	6	6	6	0	-	-
7	17	7	7	7	7	7	0	-
8	18	8	8	8	8	8	0	-
9	19	9	9	9	9	9	9	9
10	20	10	10	10	10	10	10	10

Example f: Directional selection for large size countered by failure among large individuals

1	11	1	1	1	1	1	1	1
2	12	2	2	2	2	2	2	2
3	13	3	3	3	3	3	0	-
4	14	4	4	4	4	4	0	-
5	15	5	5	5	5	0	-	-
6	16	6	6	6	6	0	-	-
7	17	7	7	7	0	-	-	-
8	18	8	8	8	0	-	-	-
9	19	9	9	0	-	-	-	-
10	20	10	0	-	-	-	-	-
