MEASUREMENT OF CONCURRENT SELECTION EPISODES

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Abstract.—Current methods for measuring selection with longitudinal data have been developed with the assumption that episodes of selection are sequential. However, a number of empirical examinations have demonstrated that natural and sexual selection may act concurrently and in opposing directions. Other recent work has highlighted the difficulty of assigning fitness values for survival when reproduction and mortality occur within a population temporally overlap. To address this problem, I formalize a method to estimate total fitness of individuals over a period of time utilizing longitudinal data. I then show how the fitness may be partitioned to provide two separate estimates of fitness for reproductive opportunity and reproductive success. In addition, another total fitness estimate for the period can be obtained from the two partitioned estimates. This procedure will allow calculation of total fitness where there are some missing datapoints for reproductive success of an individual. A simulation indicates that bias is generally low for the various fitness estimates. These methods should expand our ability to understand the interaction of different selection episodes.

Key words.—Integrative selection, measurement bias, mortality selection, partitioning fitness, residual selection, simultaneous selection, total fitness.

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A key assumption of the methodologies most commonly used to analyze selection with longitudinal data in wild populations is that selection episodes are sequential in nature; that they occur one after another without overlap (Arnold and Wade 1984a,b; Moore 1990). The generality of this assumption has not been investigated, but detailed studies of selection in experimentally manipulated environments (e.g., Endler 1980) and comparative studies (e.g., Snell et al. 1988) showed that natural and sexual selection may occur simultaneously. In populations where natural selection via mortality occurs prior to the onset of reproduction, there may in fact be a sequential nature to the episodes. However, during the period of reproduction, mortality and mating success are not truly sequential, and analyses that treat them as sequential events may be misleading.

Many episodes of concurrent selection have been inferred by manipulative experiments (e.g., Endler 1980; Reznick and Endler 1982; Reznick and Bryga 1987; Reznick et al. 1990; Johnson 2001). These methods, which often involve laboratory reproductions of natural environments (Endler 1980; Reznick and Endler 1982) or introductions of species to novel natural environments (Endler 1980; Reznick and Endler 1982; Reznick and Bryga 1987), are at times undesirable or not available for studies of natural populations. Absent the availability of these methods, investigations have been conducted using other criteria to identify natural selection during a reproductive period (Quinn and Kinnison 1999; Ruggerone et al. 2000), but the relation of these investigations to established selection theory is not clear. Other studies have assigned fitness values to the different episodes and employed classical analyses (Grether 1996; Coltman et al. 1999; Quinn et al. 2001). In this case, the overall selection may not be accurately reflected by the two separate estimates obtained for the different selection episodes (Grether 1996).

In addition to difficulties employing manipulative techniques, there is also the possibility that manipulation will not clearly separate the effects of selection via mortality and mating success. This is a result of potential changes in mating systems under heavy predation. Some mating systems are inherently risky and can lead to increased opportunity for predation (Magnhagen 1991; Berglund 1993). In these cases, the characters that are favored by natural selection may be those that are least favored by sexual selection in the absence of predation. However, the change in selection brought about by predation may not be solely due to natural selection; predation may change the mating behavior of the organism (e.g., Berglund 1993), which could lead to a different pattern of sexual selection as well. When the natural and sexual selection pressures act concurrently and in potential opposition to one another, it is important to understand the nature of the different selection episodes in order to understand the responses of the species to different habitats or environmental conditions.

As an example, consider Endler’s (1980, 1983) classic studies on Trinidadian guppies (Poecilia reticulata). Endler (1980) showed that in the absence of predation, the conspicuousness of male guppy color patterns in relation to their background was considerably higher than when predation was intense. A number of other traits also vary in a predictable manner with predation, suggesting that predation may be a principal cause of selection on these traits (Endler 1995). However, predation may not be the sole direct agent of selection causing the differences between high and low predation sites (e.g., see Reznick et al. 1996 for the other traits). Under conditions of high predation, males alter their mating behavior by seeking more sneak matings and spending less time in courtship behavior (Endler 1987; Reynolds et al. 1993; Magurran and Seghers 1994). As a result of these changes, male characteristics that increase the likelihood of successful sneak matings might be favored by selection. Hence, predation may alter the nature of selection imposed by variation in mating success; that is, sexual selection itself may differ (Partridge and Endler 1987).
A first step in allowing more extensive examination of the nature of concurrent selection episodes, and perhaps thereby obtaining a better understanding of how selection itself is changing with different environmental conditions (such as increased predation), is the development of an appropriate methodology. However, analysis of concurrent episodes of selection in this manner presents some technical difficulties. First, estimation of fitness in relation to mortality becomes more complex. Second, neither mortality nor reproductive success can be analyzed independently of the other.

Natural selection via mortality is most often measured by differential survival of an individual through a particular time period. Traditionally, survival is given some positive nonzero fitness value (usually one, e.g., Schluter 1988; Schluter and Nychka 1994) and death a fitness value of zero. However, the choice of values is complicated when the period in which natural selection is being measured overlaps with one or more breeding seasons. In this case, longevity of an individual may influence reproductive opportunity and, therefore, fitness. Consequently, the assigned fitness value must take into account the observed reproductive opportunity and how it is affected by the length of reproductive life (Brodie and Janzen 1996). Thus, mortality selection should not be measured without consideration of reproductive success. Similarly, inferences concerning selection based solely on differential reproductive success are inadequate without information on survival during reproduction.

Thus, although analysis of sequential episodes of selection requires collection of data on survival or reproductive success over time, analysis of concurrent episodes necessitates data on both of these parameters. This may be considerably restrictive in the case of selection by mortality, because direct observations are often limited and measurements of survival are often inferred solely from recaptures. In these cases, some individuals may remain alive without being recaptured (e.g., Jayne and Bennett 1990; Brodie 1992; Kingsolver and Smith 1995), and data on reproductive activity during this period may be difficult to collect.

I treat the difficulty of proper assignment of fitness values and of separating selective forces as two facets of one problem: measuring selection when episodes are not sequential in nature. I formalize a method previously used by Grether (1996) to measure total fitness where two episodes of selection occur simultaneously, specifically where one episode represents reproductive opportunity and the other represents reproductive success. I then develop a method to partition fitness in order to measure selection separately for each episode. The goal of this method is to develop appropriate fitness estimates for concurrent episodes, which will then be employed in traditional selection analyses. Finally, I analyze the potential for biases in the partitioning procedure to determine what limits the analysis may have.

**Fitness Components for Concurrent Selection Episodes**

**Total Fitness**

In general terms, I consider the case in which reproductive opportunity and reproductive success both vary simultaneously within a population. This method may be applied to single breeding seasons, or to multiple seasons. In both cases, the periods of reproductive opportunity are standardized at the level of the individual organism, rather than by calendar dates. Thus, the comparison is always between individuals at the same point in their reproductive life. For example, standardization of reproductive period for analysis of selection within a breeding season might be done based on the time of entrance to breeding grounds, establishment of a territory, or first attempt to mate for an individual. For analysis across seasons, either date of birth or the age at first reproduction may be used for each individual to signal the beginning of reproductive activity. Time of entry to breeding grounds and age at first reproduction then become traits that can be examined for potential selection. A problem with this and any other fitness analysis applied to a single breeding season of an iteroparous organism is that fitness is additive across seasons for individuals. Thus, the method developed here is most appropriately applied across the multiple breeding seasons for organisms that reproduce at more than one time during their life. The primary requirement for the analysis across multiple seasons is that the trait is consistent across seasons, or can be summarized by parameters that describe the trajectory of the trait (Lynch and Arnold 1988). This analysis is analogous to lifetime reproductive success analyses (Brommer et al. 2002), rather than the methods for measuring the intrinsic reproductive rate of individuals favored by McGraw and Caswell (1996).

Total fitness, or reproductive success, of an individual depends on the reproductive success within each given time period, and the length of residence in the breeding population. Thus, total reproductive success over the breeding season (or breeding life) for an individual is the area under a curve showing reproductive success for all the time periods an individual is reproductively active (Fig. 1A). For analytical simplicity, I have developed this in a discrete time step model, in which the length of the time periods can vary depending on the organism. The total reproductive success can be described as:

\[
W_i = \sum_{t=1}^{n} m_{i,t},
\]

where \( W_i \) is the total fitness of individual \( i \), at, \( m_{i,t} \), is the reproductive success for individual \( i \) within time period \( t \), and \( s_i \) is the breeding lifespan of individual \( i \). Time periods are measured based on the reproductive activity or birth date of individuals, not the population as a whole (for example, if two animals arrive at the breeding grounds on different days, both those days represent day one for the individual arriving then). Conversion to relative fitness is then obtained by:

\[
w_i = \frac{W_i}{W},
\]

where \( w_i \) is the relative total fitness of individual \( i \) and \( W \) is the average observed \( W_i \) in the population (Arnold and Wade 1984a).

**Partitioning Fitness**

Analyses of selection based on these measures of total fitness will accurately capture the overall effects of the com-
productive success. These terms are purely descriptive of the selection based on differential reproductive success and may mask opposing selection episodes, but may mask opposing selection episodes, specifically where one episode is due to differential opportunity to reproduce and the other is due to differential success within a period of opportunity. The terms natural selection and sexual selection are inappropriate descriptions of these two types of selection because reproductive opportunity is not solely determined by natural or sexual selection (Darwin 1859, 1871; Endler 1986; Andersson 1994; Arnold 1994). Differential opportunity to reproduce may be a result of intrasexual competition (e.g., Moore 1990). Differential reproductive success is likely to be related to sexual selection (sensu Endler 1986; Andersson 1994; but see the definition of sexual selection proposed by Arnold 1994), but since reproductive opportunity is also potentially a result of sexual selection, the terminology should be more general to the method. Therefore, for the purposes of clarity, I have used the term integrative selection to describe selection based on differential opportunity to reproduce and the term residual selection to describe selection based on differential reproductive success. These terms are purely descriptive of the methodologies employed to measure fitness below, and do not indicate a mechanism for the selection.

To illustrate the partitioning procedure, a hypothetical sample dataset for five individuals is presented in Table 1. In addition to the raw (hypothetical) data, the important transformations are illustrated. I periodically refer to the table to allow the reader to see the relatively straightforward partitioning process more clearly.

To separately measure these episodes, I use the same reproductive success and breeding longevity data for each individual that was used above to calculate total fitness, but plot the population average for each period of breeding activity:

$$\bar{m}_t = \frac{\sum_{i=1}^{n_t} m_{i,t}}{n_t},$$

where $\bar{m}_t$ is the average reproductive success for all individuals observed in period $t$, and $n_t$ is the number of individuals observed in period $t$. The population average for each period is calculated in Table 1 below the initial data on reproductive success for each individual. Integrative selection is then the extent to which phenotypic variation results in differential opportunity to reproduce, by adding or taking away from the length of time for which the area is summed (Fig. 1B). I partition fitness to reflect integrative selection by:

$$W_{i,int} = \sum_{t=1}^{n_i} \bar{m}_t,$$

where $W_{i,int}$ is the uncorrected fitness of individual $i$ relative to integrative selection. The factor of importance here is the value $s_i$, the breeding lifespan of the individual, which determines for how many periods the individual has reproductive opportunities. Another way to think of this expression is that it is the expected reproductive success for an individual present on the breeding grounds for the length of time that individual $i$ was present. The actual value is the sum of the population average reproductive success for each time period an individual is alive on the breeding grounds. In the simplified situation where there was only one time period and individuals either did or did not survive, this expression returns static 0 (died) and $\bar{m}_1$ (survived; $t = 1$, since there is only one time period) values for $W_{i,int}$. Since the value for the dead individuals is 0, this will return the same standardized estimates of fitness (see eq. 5 below) as if survivors were awarded a value of 1 (Brodie and Janzen 1996); thus, in this simplification the expression reduces to the standard value. Furthermore, where there is no reduction in $s_i$ equation (4) reduces to equal values for all individuals. In this case all individuals will have equal fitness with regard to integrative selection because their expected reproductive success will be summed over the population averages for the same number of time periods. This effectively reduces the combination of both integrative selection outlined above, and residual selection (described below) to the standard values for fitness based on reproductive success. In the hypothetical example presented in Table 1, the calculation of integrative selection is done for each individual, and presented in the summary.

**Fig. 1.** (A) The total fitness for three individuals illustrated by three different curves of reproductive success over the period of reproductive activity until death (or competitive exclusion) for each individual. Fitness is obtained by summing under each curve. (B) Schematic diagram illustrating components of reproductive success that can be classified as integrative selection (mortality or competitive exclusion) versus residual selection (mating success, fecundity, offspring survivorship, etc). The pattern of reproductive success over time is consistent with low success while establishing position or rank, peak success soon thereafter, and declining success as vigor (or value of reproduction realized for cases where multiple breeding seasons are being measured over time) declines over time. Note that this pattern, and the underlying biology, indicates a continuous function whereas the method developed herein uses discrete time intervals to summarize the data.

![Schematic diagram illustrating components of reproductive success](image-url)
values at the bottom of the table. Then, as above, we can standardize these estimates of fitness by:

$$W_{i,\text{int}} = \frac{W_{i,\text{int}}}{W_{\text{int}}},$$  \hspace{1cm} (5)$$

where $W_{i,\text{int}}$ is the relative fitness of individual $i$ in terms of integrative selection, and $W_{\text{int}}$ is the average observed $W_{i,\text{int}}$.

Residual selection can be visualized as the extent to which phenotypic variation results in raising or lowering the daily success curve for an individual (Fig. 1B). I partition fitness to reflect residual selection by:

$$W_{i,\text{res}} = \frac{\sum_{t=1}^{n} q_{i,t} m_{i,t}}{s_i} + \frac{\sum_{t=1}^{n} \sum_{m=1}^{s_{i,m}} m_{i,t}}{s_i},$$  \hspace{1cm} (6)$$

where $W_{i,\text{res}}$ is the uncorrected fitness of individual $i$ relative to residual selection, $n$ is the total number of individuals observed, and $q_{i,t}$ is the residual reproductive success for individual $i$ at time $t$ where $q_{i,t} = m_{i,t} - \bar{m}_i$. This is equivalent to determining the residual value for an individual (the first half of the expression), and using the average observation value (the quantity after the addition sign) to scale the residuals to a range of (mostly positive) values similar to those obtained for the integrative episode. Again, in the simple case in which there is only one time period and each animal either mates (1) or fails to mate (0), this process will in fact return these same values of $W_{i,\text{res}}$. In Table 1 the residual mating success for each individual for each period is provided, as well as the average of all observations. The relative fitness for each individual relative to residual selection is then obtained by:

$$W_{i,\text{res}} = \frac{W_{i,\text{res}}}{W_{\text{res}}},$$  \hspace{1cm} (7)$$

where $W_{i,\text{res}}$ is the relative fitness of individual $i$ relative to residual selection, and $W_{\text{res}}$ is the average observed $W_{i,\text{res}}$. The total fitness can then be estimated by multiplicative fitness of the two partitioned values such that

$$W_{i,\text{total}} = W_{i,\text{int}} W_{i,\text{res}}.$$  \hspace{1cm} (8)$$

This method is advantageous in that it provides an opportunity to partition fitness for measurement of multiple episodes of selection without manipulation, thus opening up the measurement of selection to more organisms where environmental or population manipulation is not a feasible technique. There are, however, some limitations to the method. First, it requires extensive sampling of individuals over time. Second, it cannot distinguish among multiple simultaneous causes of integrative or residual selection, only between the two types of selection in general. Finally, partitioning of fitness for two episodes of selection occurring simultaneously may introduce some bias into the measurements.

The potential for bias is due to the selective removal of some individuals leading to skewed estimation of reproductive success late in the breeding season (or breeding life).
Under balancing selection, this should make estimated fitness variation conservative for both integrative and residual selection (Fig. 2A). Measured reproductive success over time may decline under balancing selection. This may result in decreased integrative selection indices for those individuals with the longest breeding residence. The decline may also result in decreased residual selection indices for the individuals that survive longest. This is because the population average at that point is made up primarily from observations on individuals of similar (and not average) phenotype, reducing measured residual variation compared to the true function. When both episodes favor the same characters, the integrative fitness estimates may be artificially increased for individuals that survive longer, but the residual fitness estimates will again be conservative due to reduced residual variation (Fig. 2B). These potential biases may be more perceived than real, and should be viewed as conservative (high) estimates of the potential for bias. They may be due to induced error from the partitioning method (bias) or to the concurrence of selection itself.

One additional potential area of bias is in the estimation of total fitness from the partitioned fitness values. This calculation of total fitness assumes an accurate partitioning of fitness over an additive time period into two multiplicative fitness values. The nature and appropriateness of this partitioning can be evaluated directly by comparison with the nonpartitioned estimate of total fitness.

**Analysis of Bias**

I developed a simulation to test the bias inherent in the partitioning of fitness. An array of 1002 normally distributed individuals, with standardized phenotypes from −2.0 to 2.0 standard units in increments of 0.04 standard units, was the simulated population. Both reproductive opportunity and reproductive success were subject to directional selection. There were 21 breeding periods in the simulation, and all individuals remained in the population through the first period, hence had some reproductive opportunity. Residence on the breeding grounds was continuous from the first period of breeding for each individual until they were removed from the breeding population. Three populations were modeled simultaneously. The first was subjected to concurrent selection. The second population was subject only to residual selection, and the third was subject only to integrative selection.

I analyzed potential bias by comparing the results from the three different simulated populations. I defined the potential for integrative selection bias as the difference between the integrative selection gradients measured concurrently with residual selection and measured in the absence of residual selection. The potential for bias in residual selection was determined analogously. Bias in the total selection gradient obtained by partitioning integrative and residual selection was measured in two ways. First, I correlated the multiplicative total fitness obtained by the partitioning methodology (eq. 8) with the true total fitness (eq. 1) for each individual from the same data obtained from the concurrent selection model. Second, I calculated the total selection gradient both from fitness estimates obtained by the partitioning methodology (eq. 8), and from the true total fitness for each individual (eq. 1). I then defined the bias as the difference between the two estimates.

The various metrics used for the analysis are illustrated in Fig. 3, which is a sample of outputs from one simulation. In addition, it indicates the application of the method to analysis of a larger and more complex dataset.

The potential bias in integrative gradients is relatively low throughout most of the range of values of integrative and residual selection. Bias is generally less than 10% except where the concurrent episodes oppose one another. Where both integrative and residual selection favor the same traits, the overall effect on integrative selection gradients is to over-estimate them slightly. Where both integrative and residual selection are strong and the direction of selection differs between the two episodes, error increases up to 40%, but in this case the error is conservative; that is, the measured gradient is less than the true gradient.

The error in residual gradients is conservative in nature throughout the combinations of integrative and residual gradients examined in this analysis. The error is generally low, less than 10% over much of the range of values, but rises to about 40% at the upper limits of gradients obtained in the simulation where integrative and residual selection both cause strong selection in the same direction.

The total fitness estimates are tightly correlated over almost
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Fig. 3. Sample output from one simulation involving relatively strong opposing concurrent selection episodes. (A) The measured integrative and residual fitnesses from the model, with the measured gradients (the slopes of the regression equations) plotted above the figure legend. (B) The pattern of reproductive success of the population as a function of the period of reproductive opportunity. The decline over time is artificial in that it is induced by the death of larger, more reproductively successful individuals early in the breeding period. (C) The regression of true total fitness and estimated total fitness, with the R-square listed above the figure. (D) Integrative selection in the absence of residual selection, with the gradient listed above the figure. (E) Residual selection in the absence of integrative selection with the gradient listed above the figure. (F) The true total fitness and the estimated total fitness for each individual, with the gradients estimated for each set of data illustrated and listed above the figure legend.

The error in the total selection gradient is fairly low throughout the entire range of integrative and residual gradients. The error in the total selection gradient is fairly low throughout the range of integrative and residual gradients, less than 10% over the vast majority of values. The areas where strong integrative and residual selection of opposite sign lead to estimated total gradients around zero are the areas where the error with the greatest biological importance might result. The estimated gradients here are smaller than the true gradients, and where total selection is not strong a small bias may obscure biologically important results. More extensive details regarding this bias analysis are available from the author on request.

DISCUSSION

I have presented here a pair of related methodologies for measuring fitness where two episodes of selection are occurring simultaneously. One of the two episodes must be based on differential opportunity to reproduce (integrative selection), while the other must be based on differential reproductive success given opportunity (residual selection). The first method enables us to measure the true total fitness of an individual over time. The second allows us to partition the fitness of an individual to analyze selection separately for each episode, and to obtain an estimate of total fitness where missing data prevent application of the first method.

Brodie and Janzen (1996) point out the problem of defining appropriate levels of fitness for survival to different ages or stages. The most accurate estimation of total selection during a period of reproduction is obtained using the method described above for that purpose (sensu Grether 1996). This method provides a fitness estimate that incorporates information on the variation in reproductive success over time. A fundamental requirement of this method is a complete set of data on the reproductive success and survival of individuals throughout a breeding period or lifespan. Brodie and Janzen (1996) suggest that data this comprehensive may be rare, hence the applicability of this method for measurement of total selection may be somewhat limited to a few studies of extraordinarily high quality (e.g., red deer, Cervus elaphus, Clutton-Brock et al. 1997; Soay rams, Ovis aries, Coltman et al. 1999; Darwin’s finches, Geospiza spp., Grant and Grant 2002).

The second methodology, involving partitioning of integrative and residual fitness estimates, offers opportunities to more thoroughly examine the different selection episodes that lead to the observed overall selection. Furthermore, the partitioning methodology can be used to obtain total fitness estimates over a period of time when complete data on reproductive success is not available. It is still necessary to have accurate data on time of entry to the breeding grounds or age at first reproduction, as well as time of death or removal from the breeding population. However, if only partial data on reproductive success within the intervening time periods are available, it is still possible to partition fitness. The popu-
lation mean reproductive success will then be based on fewer samples, and individual residual fitness will be based on a subset of datapoints rather than on complete data including each reproductive period for the life of the individual. Residual selection and total selection can then be calculated only from animals for which one or more reproductive success estimates were obtained. Integrative selection analyses could still take advantage of the entire group for which breeding lifespan is known, using the population averages for reproductive success to provide improved fitness estimates. Thus, total fitness can be estimated for any individual for whom some reproductive success information is present, and integrative fitness can be estimated for any individual for whom lifespan data are available. This may help to solve one of the problems biologists face by allowing appropriate use of limited data to make biologically realistic inferences about fitness and selection (Brodie and Janzen 1996). A companion paper illustrates the use of this technique to analyze selection in a semelparous organism, sockeye salmon (Oncorhynchus nerka) in which partial reproductive success information is available from some members of the population (Hamon and Foote 2005). Other investigators also have datasets that might produce interesting new insights by application of this method (e.g., Kruuk et al. 2001).

My approach does not attempt to address the changes in variance of trait values and fitness over the course of time in question. A number of examinations of this problem for studies of multiple sequential episodes have been undertaken (e.g., Koenig and Albano 1987; Conner 1988; Wade and Kalisz 1989; Koenig et al. 1991; Schluter et al. 1991; Preziosi and Fairbairn 2000). Because in some, or perhaps most, populations differential survival will lead to diminishing sample size at later breeding stages, this problem might also lead to bias in my method. However, there is a fundamental difference in that my method does not analyze data separately across multiple, sequential episodes. Instead, the increases in variation are only for the estimates of survival value and residual success for some breeding periods of longer-lived individuals. These individuals’ estimates of fitness will be based on more datapoints than for individuals that do not survive as long, which should in fact act to decrease the error in their overall fitness scores, even while uncertainty in the incremental changes to their scores increases. Whether the increases in variance are still sufficient to result in bias is not clear, but within the concurrent selection episodes in question these two forces (increasing variance against increasing sample size) should lead to fewer variance problems than across multiple, sequential episodes. Of course, the combination of fitness data from previous episodes of selection with data from concurrent episodes as outlined here will result in the same problems of changes in trait and fitness variance that have been observed previously. But since this technique merely provides fitness values for use in traditional analyses, addition of other sequential episodes of selection can also be accompanied by use of techniques to evaluate the effects of changes in variance on the results.

The fitness estimates generated by this method are more closely related to lifetime fitness measurements (Brommer et al. 2002) rather than fitness measures tied to intrinsic reproduction rates (McGraw and Caswell 1996). For iteroparous organisms, this distinction may be important, and authors should consider carefully the potential effects of this on their analysis (e.g., van Tienderen 2000; Brommer et al. 2002). A useful extension of this work in the future would be to develop the estimates of reproductive success in the framework of intrinsic reproduction rates (McGraw and Caswell 1996), sensitivities (Lande 1982), or elasticities (van Tienderen 2000).

With these caveats, the simulation indicates that the estimates of fitness derived by my method produce satisfactory results when employed in traditional selection analyses. There is some bias in the integrative and residual gradients. This bias appears to increase as the strength of selection increases. In most cases, this bias is conservative; that is, it tends to result in a measured gradient closer to zero than the equivalent gradient in one of the parallel populations. The primary exception to this trend is that the integrative gradient becomes slightly exaggerated where the two selection episodes favor the same trait. The predominance of conservative biases suggests that gradients can be appropriately reported. Some final caveats on the use of this methodology are that, as yet, I have not tested the potential for bias or error in estimation of quadratic or correlational gradients and that the analyses of bias that are presented here are based on only one type of population model. Other models may provide somewhat different biases. Nevertheless, based on my analyses, these methodologies represent an opportunity to study some dynamic selection episodes that were previously not fully open to investigation in wild populations. Additionally, the terms integrative selection and residual selection are new to this analysis. They are not descriptive of any particular mechanisms of selection, but instead merely represent ways of measuring fitness. As a result, authors may choose to label these episodes as natural or sexual selection if they have evidence as to the mechanism of selection that is responsible for each episode.

Finally, to employ one or both of these methods successfully, minimum requirements must be met. First, measures of phenotype (or genotype) must be taken for each individual. Second, the time period in which each individual becomes reproductively active must be recorded. Third, reproductive success information for each period for each individual should be recorded; missing data here will limit the analysis, but sufficient data will still permit the investigator to analyze selection based on partitioned selection gradients. Finally, the time period in which each individual ceases breeding activity must be known. With these data in hand, traditional selection analyses can be performed using fitness estimates derived herein. A spreadsheet that automates the application of these formulae is available from the author to facilitate calculation of the different fitness estimates.

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