

# Relative Fitness, Teleology, and the Adaptive Landscape

John O. Reiss

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**Abstract** The metaphor of the adaptive landscape, introduced by Sewall Wright in 1932, has played, and continues to play, a central role in much evolutionary thought. I argue that the use of this metaphor is tied to a teleological view of the evolutionary process, in which natural selection directs evolution toward an improved future state. I argue further that the use of “relative fitnesses” standardized to an arbitrary value, which is closely connected with the metaphor of an adaptive landscape, produces a disconnect between the mean fitness of a population and any real property of that population. This allows for a vague and ill-defined improvement to occur under the influence of selection. Instead, I suggest that relative fitnesses should be standardized by the mean absolute fitness (expected population growth rate), so that they express the expected rate of increase in frequency, rather than number. Under this definition, the mean relative fitness of all populations is always 1.0, and never changes as long as the population continues to exist.

**Keywords** Fitness landscape · Adaptation · Fisher · Fundamental theorem of natural selection

...something is very wrong with population geneticists’ obsession with the mean fitness of a population.  
(J.H. Gillespie, 1991)

## Introduction

The theory of natural selection, as introduced by Darwin (1859), was formulated entirely in terms of verbal models. With the rediscovery of Mendel’s work around 1900 the path was open to develop an explicit, quantitative model of natural selection in terms of population genetics (see Gayon, 1998; Provine, 1971). Beginning with the early work of Fisher, Haldane, and Wright, the field of population genetics has developed into one of great mathematical sophistication. However, the basic (“paradigmatic” in the sense of Kuhn, 1970) models used are rather simple. In such models, natural selection is represented as variation in fitness among genotypes (e.g., Hartl & Clark, 1997; Hedrick, 2000), with fitness defined as “the relative ability of different genotypes to pass on their alleles to future generations” (Hedrick, 2000, p. 90). The rigor of this approach, however, is lessened because there is as yet no universally agreed upon measure of fitness; fitness is either defined metaphorically, or defined only relative to the particular model or system used. It is fair to say that due to this lack, there is still no real agreement on what exactly the process of natural selection is. This is clearly a problem.

Historically, this problem can be traced back to the controversy between R. A. Fisher and Sewall Wright over the proper way to model the evolutionary process (Gayon, 1998; Provine, 1986). Because the mathematics of the more sophisticated population genetic models are complicated, and the parameters of these models are almost never measurable directly in experimental or natural populations, metaphors have perhaps played a greater role in evolutionary biology than in most other sciences. The controversy between Wright and Fisher is embodied in the contrast between Wright’s popular metaphor of a “surface of selective value,” or adaptive landscape, on which

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J. O. Reiss (✉)  
Department of Biological Sciences, Humboldt State University,  
Arcata, CA 95521, USA  
e-mail: jor1@humboldt.edu

populations evolve (e.g., Wright, 1932, 1969, 1988), and Fisher's "fundamental theorem of natural selection" which states that "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher, 1930, p. 35).

In a comprehensive review of the fundamental theorem, Edwards (1994) showed that Wright misinterpreted the fundamental theorem as supporting his own metaphor of the adaptive landscape. He showed further that Wright's metaphor is fundamentally flawed, as had been previously pointed out by Fisher (1941) and Provine (1986), among others. Nevertheless, Edwards noted that "the metaphor was powerful enough to ensure that even the criticism of Fisher (1941) had no effect" (p. 460). Edwards was certainly overly optimistic in speaking of the "rise and fall" of the adaptive landscape; because current textbooks continue to include this metaphor, although usually with some reservations (e.g., Freeman & Herron, 2007; Futuyma, 2005; Ridley, 2004). Moreover, it appears that the adaptive landscape has recently been undergoing a resurgence, with explicit use ranging from the evolution of quantitative traits (e.g., Arnold, 2003; Arnold, Pfrender, & Jones, 2001; Lande & Arnold, 1983), to protein evolution (e.g., Bershtein, Segal, Bekerman, Tokuriki, & Tawfik, 2006; Kauffman, 1993; Kauffman & Levin, 1987; Orr, 2006), to the theory of speciation (Gavrilets, 2004).

Ten years ago, Coyne, Barton, and Turelli (1997) presented a critique of Wright's "shifting balance" theory of evolution based on both theoretical and empirical considerations. They argued that there was no evidence that this process, as Wright conceived it, ever occurred in natural populations, let alone constituted the major process underlying adaptive evolution. This challenge to the utility and applicability of Wright's theory initiated a lively debate (Coyne, Barton, & Turelli 2000; Goodnight & Wade, 2000; Peck, Ellner, & Gould, 1998, 2000; Wade & Goodnight, 1998), with other authors defending the value, if not the universal validity, of Wright's theory.

Wright's shifting-balance theory is of course closely connected to his metaphor of a "surface of selective value," or adaptive landscape, on which populations evolve (Wright, 1932, 1969, 1988). More specifically, this metaphor posits an adaptive landscape that consists of many "adaptive peaks" of different height, separated by "adaptive valleys." Natural selection tends to drive populations up a peak, but it may be only a local peak, not a global peak in the landscape. As Wright saw it, this is a problem with the process of natural selection. He believed that this problem could be solved by the shifting balance process. In the shifting balance process, genetic drift in local populations causes them to lose fitness and shift across an adaptive valley toward the domain of attraction of a new adaptive peak. Selection within these local

populations causes them to ascend the new peak. Finally, those populations that have reached higher peaks send out more migrants than those on lower peaks, converting the entire species to that peak.

Strangely, in the debate over the shifting-balance theory the validity of the associated metaphor of the adaptive landscape was never explicitly raised, and no reference was made to the Wright/Fisher controversy. In the present paper, I argue that the problem for which Wright conceived the shifting balance process as a solution does not exist, whatever the merits of the process itself. I argue further that Wright's perception of this problem depends on a teleological view of evolution, and that the metaphor of the adaptive landscape itself is fundamentally and unavoidably a teleological one, at least when applied to the evolution of species in nature.

The validity of teleological explanations in biology in general has been much debated, with at least some authors considering them justifiable in certain contexts (see Allen, Bekoff, & Lauder, 1998). Nevertheless, I do not believe anyone today would wish to defend a view in which a future state of a population or species actively drives the evolutionary process toward its own attainment. I will argue that the teleology inherent in the metaphor of the adaptive landscape consists in considering the adaptedness of a population to be relative to a *future* state that it might attain, with natural selection then acting as a force driving the population toward this improved future state. With an absolute standard to measure improvement (and a deterministic evolutionary process) this might be acceptable; I argue that no such standard exists.

In particular, I argue that there is no way to make any reasonable sense of the scale on which the height of adaptive peaks is measured. Since this scale is a scale of "fitness," I first examine the meaning of fitness as it is used in standard population genetic models of evolution. I show that the measure of "relative fitness" commonly used has allowed relative fitness to take on some of the associations proper to absolute fitness. I argue that it is the disconnection between mean relative fitness and any observable trait of a population that has allowed a teleological view of evolution to enter the basic equations of population genetics. From an historical perspective, it appears that this teleology derives directly from Sewall Wright. I next turn to examining this history, and show how the origin and development of Wright's metaphor of an "adaptive landscape" involves a teleological view of evolution. I conclude by comparing Wright's metaphor to Fisher's "Fundamental theorem of natural selection." While this theorem superficially seems to incorporate a teleological view similar to Wright's, a careful examination shows that in fact it does not. Parts of this discussion have been anticipated by Edwards (1994), Ruse (1996),

and Gayon (1998), though each from a rather different perspective.

I must apologize in advance for what may seem a rather laborious and tedious treatment to some. My own training is as an evolutionary morphologist, and I can not claim any special facility or familiarity with the mathematics involved. Rather, this paper grew out of my own struggle to make sense of the term “adaptation” as used in evolutionary morphology, which led eventually to a consideration of population genetic models, as the most explicit formulations of the process of natural selection available. The analysis is not intended to be particularly novel or sophisticated, but rather to point out obvious and simple relations that can be lost in more sophisticated treatments.

### Rate of Increase

In order to understand the teleological underpinnings of the adaptive landscape, it is necessary to first consider the scale on which the height of adaptive peaks is measured, or ‘fitness.’ However, because of much controversy over the proper definition of ‘fitness’, and various associations the term may have, I will initially avoid this term, instead framing my discussion in terms of the *rate of increase* (Fisher, 1930) of lineages. This will then allow me to examine the relation of fitness to rates of increase.

I will concern myself solely with what one might call ‘evolutionarily closed populations.’ These are populations consisting of reproducing entities (organisms, genes, etc.), defined such that:

- The population is examined over a given time period,  $t$ , with initial population size  $N(0)$  and final population size  $N(t)$ .
- At time 0, all ancestors of members of the population at time  $t$  were members of the population (no immigration).
- Each of the  $i$  members of the population at time 0 has a definite number of descendants in the population at time  $t$ ,  $N_i(t)$ , such that  $\sum N_i(t) = N(t)$  (a principle of conservation of inheritance).

In such a population, the simplest measure of success is simply the number of descendants of an initial member of the population at some later time  $t$ , or  $N_i(t)$ . This measure has the advantage that it expresses an objectively defined feature of the population, which deterministically connects the initial state of the population with its final state. Since over multiple generations neither organisms nor genes continue to exist, but rather only organismic and genetic *lineages* do, the number of surviving descendants is a measure of the degree to which the *lineage* founded by the

$i$ th member of the population at time 0 is satisfying its conditions for existence (Reiss, 2005). Expressed per interval of time, this number is what I will call the *rate of increase*  $R_i = N_i(t)/t$  of the  $i$ th lineage. I will show that standard measures of differential survival and reproduction can be directly related to this measure.

The simplest way to see how one can measure rates of increase is to construct some hypothetical examples of populations. In particular, we want to represent a population of individuals (organisms) carrying genes that are inherited in Mendelian fashion. This is the basic population genetic model, which—as most have recognized—provides a rigorous framework within which to construct a system of measurement of rates of increase. Through my analysis of some simple situations, I will develop a consistent system of derived measures based on individual lineage rates of increase. These include measures of average rate of increase, relative rate of increase, multiple-population average rates of increase, and rates of increase in sexual diploids (single and multi-locus). It is these derived measures that can be most usefully compared with the various definitions of ‘fitness’ that have been proposed.

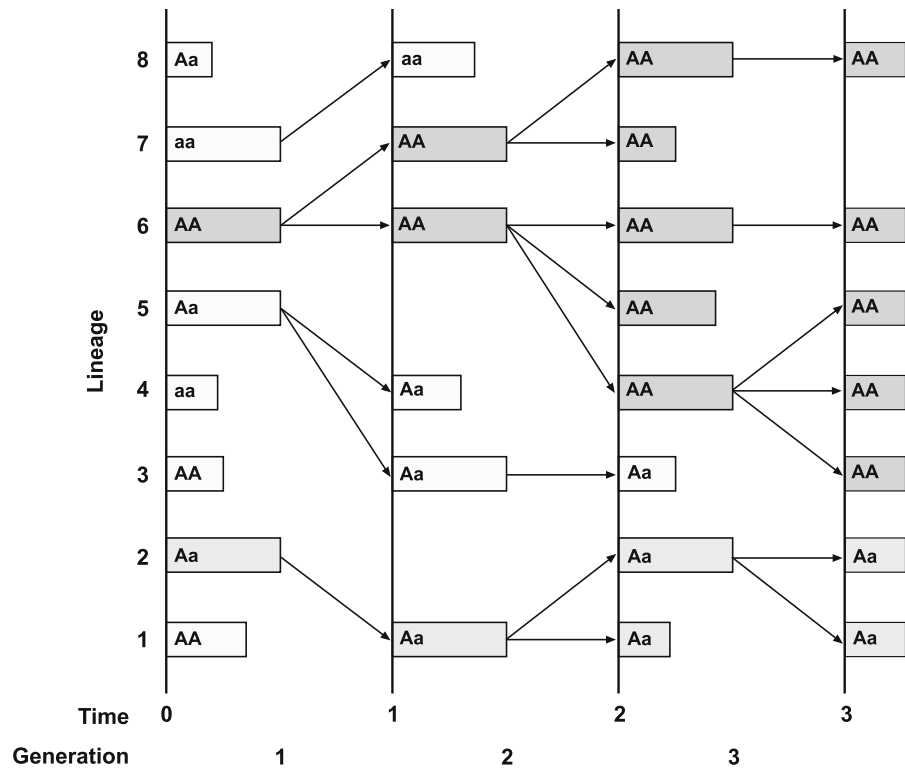
### Absolute Rates of Increase in Clonal Populations

To begin with, let us examine an example (Fig. 1, Table 1) of a single genetic locus in an asexual (clonal) population of diploid, multicellular organisms with discrete generations. In the terminology defined above, we can conceive of this as two coexistent populations, one of organisms, one of genes, with two genes mapping to one organism. This example represents three generations; for organisms the initial population size is eight and the final population size is seven, for the genes they are 16 and 14, respectively. Only two types of events occur in this time period: reproduction and death.

The genetic (allelic) lineages each have the same rate of increase as the corresponding organismal (and genotypic) lineage in this simple clonal case, so for now there is no need to treat them separately. Applying the measure of rate of increase, number of descendants, to the organismal lineages we find that in this example only two of these still exist at time 3; lineage 2 has two descendants, lineage 6 has five. Since we are interested in *rates* of increase, however, we must express these as a rate of increase of two and five *per three generations*, respectively. All other lineages have a rate of increase of 0 (per three generations).

We can define the rate of increase of a lineage over a single generation as the number of descendants at the end of the period divided by the number at the beginning. More formally, if  $R_i(t)$  is the rate of increase of the  $i$ th lineage from time  $t$  to time  $t + 1$ , then  $R_i(t) = N_i(t + 1)/N_i(t)$ . With this definition, the rate of increase of a lineage over

**Fig. 1** Schematic representation of a clonal population of diploid organisms over three discrete generations. The genotype at a single locus is shown. For calculations of representative rates of increase for this population, see Table 1



**Table 1** Representative rates of increase for the population of Fig. 1

Variable		Generation				Total/ 3 Gen	Mean/ Gen ( $\bar{G}$ )
		1	2	3	4		
Absolute lineage rate of increase ( $R_i$ ) (shown for lineages 2, 5, and 6 only)	$R_2$	1.00	2.00	1.00		2.00	1.26
	$R_5$	2.00	0.50	0.00		0.00	0.00
	$R_6$	2.00	2.50	1.00		5.00	1.71
Initial genotype numbers ( $N_{ab}$ )	$N_{AA}$	3	2	5	5		
	$N_{Aa}$	3	3	3	2		
	$N_{aa}$	2	1	0	0		
Absolute genotypic rate of increase ( $R_{ab}$ )	$R_{AA}$	0.67	2.50	1.00		1.67	1.19
	$R_{Aa}$	1.00	1.00	0.67		0.67	0.87
	$R_{aa}$	0.50	0.00	0.00		0.00	0.00
Initial population size ( $N$ )		8	6	8	7		
Mean absolute rate of increase ( $\bar{R}$ )		0.75	1.33	0.88		0.88	0.96
Initial genotype frequencies ( $f_{ab}$ )	$f_{AA}$	0.38	0.33	0.63	0.71		
	$f_{Aa}$	0.38	0.50	0.38	0.29		
	$f_{aa}$	0.25	0.17	0.00	0.00		
Relative genotypic rate of increase ( $r_{ab}$ )	$r_{AA}$	0.89	1.88	1.14		1.90	1.24
	$r_{Aa}$	1.33	0.75	0.76		0.76	0.91
	$r_{aa}$	0.67	0.00	0.00		0.00	0.00
Mean relative rate of increase ( $\bar{r}$ )		1.00	1.00	1.00		1.00	1.00

several generations is simply a multiple of its rate of increase over each generation. Thus lineage 6 has a rate of increase of 2.0 (2/1) in the first generation, 2.5 (5/2) in the second generation and 1.0 (5/5) in the third generation,

giving  $(2/1)(5/2)(5/5) = 5$  per three generations (see Table 1).

The average per generation rate of increase of each lineage is calculated as the cube root of its rate over three

generations (the *geometric mean*), giving an average for lineage 6 of 1.71 per generation. The geometric mean must be used because it is the average rate that gives the lineage its actual number of descendants at the end of the period. In general, we see that the mean rate of increase of this lineage ( $G_{Ri}$ ) is given by

$$G_{Ri} = \sqrt[m]{\prod_{t=0}^{m-1} R_i(t)} = \sqrt[m]{\frac{N_i(m)}{N_i(0)}} \quad (1)$$

where  $N_i(t)$  is the number of individuals in the  $i$ th lineage at time  $t$ , and  $m$  is the total number of generations.

Rather than measuring the rate of increase of each individual lineage, one might want to measure the average rate of increase of all lineages sharing some characteristic, e.g., a given genotype at a locus. From time  $t$  to  $t + 1$ , the mean rate of increase for those lineages of a particular genotype,  $ab$ , is given by

$$R_{ab}(t) = \frac{\sum_{i \in ab} N_i(t) R_i(t)}{\sum_{i \in ab} N_i(t)} = \frac{\sum_{i \in ab} N_i(t+1)}{\sum_{i \in ab} N_i(t)} = \frac{N_{ab}(t+1)}{N_{ab}(t)} \quad (2)$$

or in words, by the total number of  $ab$  individuals at the end of the period divided by the total number at the beginning. Note that for this average one uses the *arithmetic* mean of the individual lineages.

The geometric mean per generation rate of increase for all  $ab$  lineages can be calculated similarly to that for an individual lineage:

$$G_{R_{ab}} = \sqrt[m]{\prod_{t=0}^{m-1} R_{ab}(t)} = \sqrt[m]{\frac{N_{ab}(m)}{N_{ab}(0)}} \quad (3)$$

Finally, note that the average rate of increase of the population is simply the population growth rate:

$$\bar{R} = \frac{\sum_i N_i(t) R_i(t)}{\sum_i N_i(t)} = \frac{N(t+1)}{N(t)}. \quad (4)$$

### Relative Rates of Increase

All of the derived rates of increase examined so far might be called *absolute rates of increase* (by analogy with “absolute fitnesses”) since they reflect the increase or decrease in numbers of one or more lineages in terms of the absolute number of descendants present at a later time. In some cases, one might be more interested in the *relative rates of increase* of distinct lineages or groups of lineages. Such relative rates of increase can be thought of as the rate of increase or decrease in *frequency*, rather than number, or

alternatively, as the rate of increase compared with that of the population as a whole. For an individual lineage, we can define the relative rate of increase as

$$r_i(t) = \frac{f_i(t+1)}{f_i(t)} = \frac{R_i(t)}{\bar{R}(t)} \quad (5)$$

where  $r_i(t)$  is the relative rate of increase of lineage  $i$  from time  $t$  to  $t + 1$ ,  $f_i(t)$  is the frequency of members of  $i$  at time  $t$  [ $= N_i(t)/N(t)$ ], and  $\bar{R}(t)$  is the absolute population rate of increase (growth rate). Averages across lineages and generations can be calculated similarly to those for absolute rates of increase:

$$G_{r_i} = \sqrt[m]{\prod_{t=0}^{m-1} r_i(t)} = \sqrt[m]{\frac{f_i(m)}{f_i(0)}} \quad (6)$$

$$r_{ab}(t) = \frac{\sum_{i \in ab} f_i(t) R_i(t)}{\sum_{i \in ab} f_i(t)} = \frac{f_{ab}(t+1)}{f_{ab}(t)} = \frac{R_{ab}(t)}{\bar{R}(t)} \quad (7)$$

$$G_{r_{ab}} = \sqrt[m]{\prod_{t=0}^{m-1} r_{ab}(t)} = \sqrt[m]{\frac{f_{ab}(m)}{f_{ab}(0)}} \quad (8)$$

Note that the average *relative* rate of increase of all lineages,  $\bar{r}(t)$ , is always unity, since the population as a whole neither increases nor decreases in frequency.

### Multiple Populations

For a single population, it is clear from Eq. 4 that there is no conflict between relative and absolute perspectives, since for all possible subpopulations relative and absolute rates of increase have a constant ratio of  $1 : \bar{R}(t)$  from time  $t$  to  $t + 1$ . However, when one considers averages of within population values across multiple populations, conflicts between the two perspectives do arise (cf. Gillespie, 1977; Karlin & Lieberman, 1974).

For a set of  $j$  populations, define the average within population number and frequency of a class of lineages (e.g., of a given genotype,  $ab$ ) as

$$\bar{N}_{ab}(t) = (1/j) \sum_j N_{abj}(t) \quad (9)$$

and

$$\bar{f}_{ab}(t) = (1/j) \sum_j f_{abj}(t) \quad (10)$$

where  $N_{abj}(t)$  is the number of individuals of  $ab$  lineages in the  $j$ th population at time  $t$ , and  $f_{abj}(t)$  is the corresponding

frequency (note that Eq. 9 is an *unweighted* average of these frequencies). If we then define the average within population absolute rate of increase as

$$\bar{R}_{ab}(t) = \frac{\sum_j N_{abj}(t) R_{abj}(t)}{\sum_j N_{abj}(t)} = \frac{\sum_j N_{abj}(t+1)}{\sum_j N_{abj}(t)} \quad (11)$$

and the average relative rate of increase as

$$\bar{r}_{ab}(t) = \frac{\sum_j f_{abj}(t) r_{abj}(t)}{\sum_j f_{abj}(t)} = \frac{\sum_j f_{abj}(t+1)}{\sum_j f_{abj}(t)} \quad (12)$$

where  $R_{abj}(t)$  is the average rate of increase of  $ab$  lineages in the  $j$ th population (2), and  $r_{abj}(t)$  the equivalently defined relative rate of increase (note that these are both weighted averages, but with the absolute value weighted by numbers (per capita), while the relative value is weighted only by frequency), then it can be shown that

$$\bar{N}_{ab}(t) = \bar{N}_{ab}(0) \left[ \prod_{t=0}^{m-1} \bar{R}_{ab}(t) \right] \quad (13)$$

and

$$\bar{f}_{ab}(t) = \bar{f}_{ab}(0) \left[ \prod_{t=0}^{m-1} \bar{r}_{ab}(t) \right] \quad (14)$$

or in words, that *the average number/frequency of  $ab$  individuals at any time is the product of their average initial number/frequency and the average absolute/relative rate of increase of their descendant lineages up to that time*, just as in a single population.

Nevertheless, it can also be shown that with these definitions

$$\bar{f}_{ab}(t) \neq \bar{N}_{ab}(t) / \bar{N}(t) \quad (15)$$

or in words, that *the average within population frequency of  $ab$  individuals is not (in general) equal to the average number of  $ab$  individuals in each population divided by the average population size*.

This discrepancy between absolute and relative perspectives is a challenge to the consistency of the system we are constructing. It is this discrepancy, in fact, that led Gillespie (1977) to describe a “new evolutionary principle” of selection for variance in offspring number. He noted that under the above definitions (Eqs. 9–12), two groups of lineages with the same average absolute rate of increase do not necessarily have the same average relative rates of increase, and that the group with the lowest variance in absolute rate of increase has the highest average relative rate of increase. In his words:

The addition of a stochastic element to the offspring *number* of a genotype will effectively lower the fitness of that genotype as measured by its mean *frequency* in the next generation. (p. 1012, emphasis added)

This is true, however, only for the above definitions of average frequency and relative rate of increase (Eqs. 10, 12). Under an alternative definition of these quantities, this discrepancy disappears. Instead of using Eqs. 10 and 12, we can define the average frequency of a group of lineages as

$$\bar{f}_{ab}(t) = \frac{\sum_j f_{abj}(t) N_j(t)}{\sum_j N_j(t)} = \frac{\sum_j N_{abj}(t)}{\sum_j N_j(t)} \quad (10a)$$

and the average relative rate of increase as

$$\bar{r}_{ab}(t) = \frac{\sum_j r_{abj}(t) N_{abj}(t) \bar{R}_j(t) \sum_j N_j(t)}{\sum_j N_{abj}(t) \sum_j \bar{R}_j(t) N_j(t)} = \frac{\bar{R}_{ab}(t)}{\bar{R}(t)} = \frac{\bar{f}_{ab}(t+1)}{\bar{f}_{ab}(t)} \quad (12a)$$

where  $\bar{R}_j(t)$  is the increase (growth) rate of the  $j$ th population from time  $t$  to  $t+1$ , and  $\bar{R}(t)$  is the average population growth rate. Now not only do Eqs. 13 and 14 hold, but it can also be shown that

$$\bar{f}_{ab}(t) = \bar{N}_{ab}(t) / \bar{N}(t) \quad (15a)$$

This is none too surprising, as the average frequency calculated is now the *per capita* weighted frequency, and the many separate populations are effectively being treated as a single large population.

We are faced with a choice of two alternative sets of definitions: those of Eqs. 10 and 12 versus those of Eqs. 10a and 12a. Of course there is really no necessity of choosing, we could simply give these two different names. Nevertheless, since I am trying to construct a *consistent* set of derived quantities, I believe Eqs. 10a and 12a to represent a more useful definition. In a nutshell, I am choosing to define the average frequency of a class of lineages as the average frequency *experienced by individual members of each class*, rather than the average frequency *within each population* (in the single population case these are of course the same).

## Sexual Diploid Populations, Discrete Generations

The phenomenon of sex is an immensely complicating factor in the consideration of rates of increase. In a sexual population, no longer is it true that organismal lineage rates of increase are the same as genetic (allelic) lineage rates of



increase. In fact, it is not clear what one even means by organismal lineages, as the genetic lineages carried by an organism separate and mix with others in meiosis and conjugation. Even in the clonal case, it is really not true that organisms form lineages—only certain cellular subpopulations form lineages, which are really *cellular* lineages (see Buss, 1987). With sex even these cellular lineages intermix. Nevertheless, the measures of rate of increase defined above can be extended to sexual populations, by focusing on the increase of *allelic* lineages.

Consider the population of Fig. 2 (and Table 2). This represents three generations of a sexual, diploid population with discrete generations; two loci are represented. With reference to the population of *alleles*, it is clear that conditions a–c above are fulfilled: there is a definite population size (number of alleles) at each time,  $N(t)$ , there is no immigration, and each of the  $i$  alleles present at time 0 has a definite number of descendants at time  $t$ , such that  $\sum N_i(t) = N(t)$ , where  $N_i(t)$  is the number of alleles in the  $i$ th lineage at time  $t$ . Because this allelic population is isomorphic with the asexual population treated in Eqs. 1–15, all of these equations still apply.

For various reasons, however, most people are more interested in organisms than alleles. Given the realities of Mendelian inheritance, it is clear that organisms only persist past their death as genes, or genetic lineages. It seems reasonable to define an organismal lineage as being composed of all the genetic (allelic) lineages carried by that organism, and the rate of increase of such an organismal lineage as the average rate of increase of these genetic lineages. This measure is obviously relative to the loci considered (only two are represented in Fig. 2).

The “true” rate of increase of an organismal lineage might be defined as that which is averaged over all loci, but the determination of values for all loci is an extremely difficult, perhaps impossible task, and it raises troubling questions about how to define a locus. In most cases it will be both more useful and more practical to determine values with respect to only a few loci (e.g., a gene region or regions) under study. With respect to a single locus occupied by allelic lineages  $ia$  and  $ib$ , the absolute rate of increase of the  $i$ th organismal lineage is

$$R_i(t) = [R_{ia}(t) + R_{ib}(t)]/2 \quad (16)$$

and with respect to  $n$  loci it is

$$R_i(t) = (1/2n) \sum_{k=1}^n [R_{ika}(t) + R_{ikb}(t)] \quad (17)$$

where  $R_{ika}(t)$  is the rate of increase of the  $a$ th allele at the  $k$ th locus.

Because of the nature of biparental reproduction, in the first generation  $R_i(t)$  will be the same for all loci (and equal to one-half the number of offspring of  $i$ ), but after this it will vary among loci. Since  $R_i(t)$  is only a particular type of average across lineages, Eqs. 16 and 17 are just applied versions of Eq. 2. Extension to other averages is easily made, with absolute rates of increase for lineages derived from ancestors of particular single locus genotypes being given by

$$R_{ab}(t) = \frac{\sum_{i \in ab} [R_{ia}(t) + R_{ib}(t)]}{N_{ab}(t)} \quad (18)$$

where  $N_{ab}(t)$  is the number of alleles present at time  $t$  derived from an ancestor in the initial population of genotype  $ab$  (not the number of alleles present in  $ab$  genotype individuals). For multiple-locus genotypes we have, similarly,

$$R_{1a1b2a2b\dots}(t) = \frac{\sum_{i \in 1a1b2a2b\dots} \sum_{k=1}^n [R_{ika}(t) + R_{ikb}(t)]}{N_{1a1b2a2b\dots}(t)} \quad (19)$$

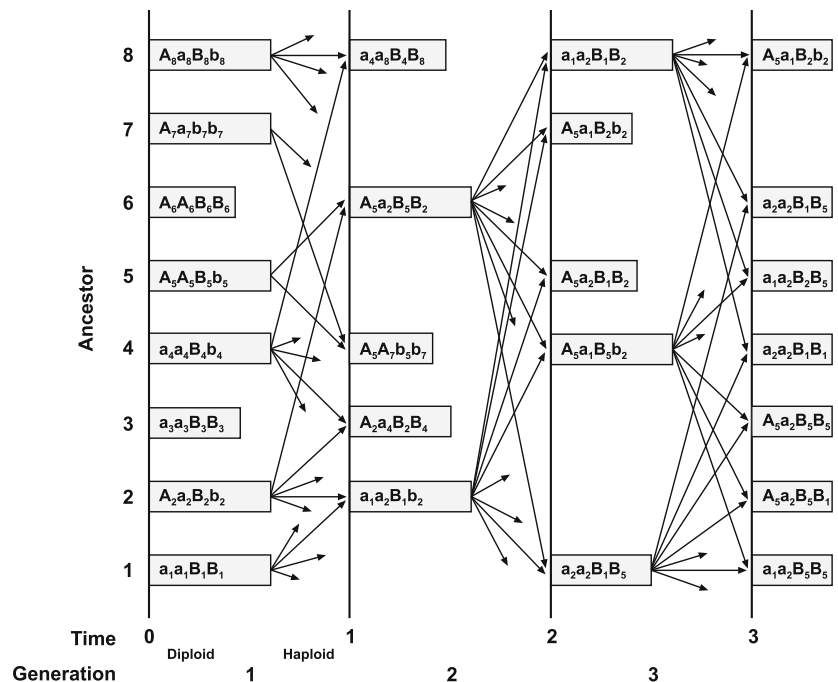
where  $n$  is the total number of loci, and  $N_{1a1b2a2b\dots}(t)$  is the number of alleles present at time  $t$  derived from an ancestor of genotype  $1a1b2a2b\dots$ . The equivalent relative rates of increase can of course be found by dividing by  $\bar{R}(t)$ .

### Overlapping Generations, Continuous Time

Finally, we can examine the situation in a similar diploid population with overlapping generations (Fig. 3, Table 3). Since our measures of organismic rates of increase are defined in terms of allelic rates of increase, and allelic lineages are just as continuous when generations overlap as when they are discrete, there is no difficulty using Eqs. 16–19 for continuous time populations, with  $t$  now representing astronomical time, rather than generations.

If we want to consider all members of the initial population as diploids, we must adopt a convention that haploid individuals (e.g., gametes) are only counted as new lineages if they are going to pair with other haploids. Of course, with overlapping generations all members of the initial population are not the same age (with the convention suggested, some are in fact represented by haploids), and one may feel it rather unreasonable to define an average rate of increase across organisms of all ages in the initial population. In a large enough population, there is no reason why one cannot derive average rates of increase for particular age classes within each genotype.

**Fig. 2** Schematic representation of a sexual population of diploid organisms over three discrete generations. The genotype at two loci is shown. Alleles are numbered with respect to the ancestor in the initial population ( $t = 0$ ) in which they are found. For calculations of representative rates of increase for this population, see Table 2



### Fitness in Population Genetics

Having defined quantities measuring the rates of increase of various lineages, we are prepared to consider the relation

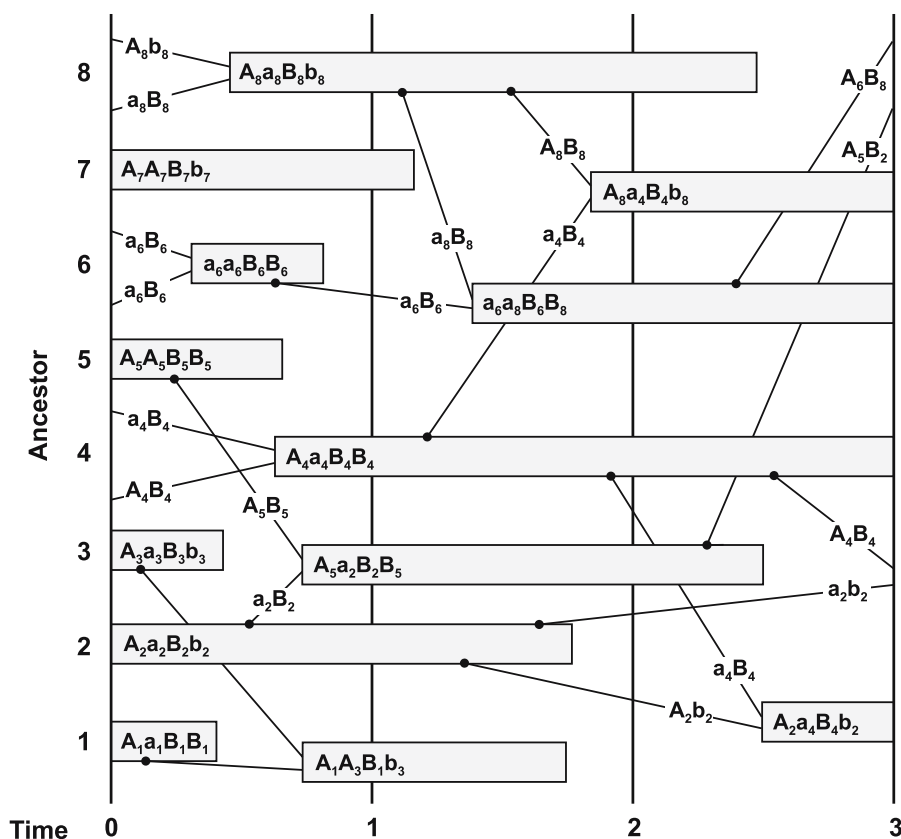
between these quantities and that quantity commonly called “fitness” in population genetics. The volume of literature discussing the true meaning of fitness in evolutionary biology is remarkable. Nevertheless, among

**Table 2** Representative rates of increase for the population of Fig. 2

Variable		Generation				Total/ 3 Gen	Mean/ Gen ( $\bar{G}$ )
		1	2	3	4		
Absolute allelic rate of increase ( $R_{ia}$ ) (shown for ancestor 2 only)	$R_{2A}$	1.00	0.00	0.00		0.00	
	$R_{2a}$	2.00	2.00	2.00		8.00	2.00
	$R_{2B}$	2.00	1.50	0.67		2.00	1.26
	$R_{2b}$	1.00	2.00	0.50		1.00	1.00
Absolute organismic lineage rate of increase ( $R_i$ ) (shown for ancestors 2 and 5)	$R_2$	1.50	1.38	0.79		1.64	1.18
	$R_5$	1.00	1.25	2.00		2.50	1.36
Initial number of alleles derived from genotype $ab$ lineages ( $N_{ab}$ )	$N_{AA}$	4	2	3	3		
	$N_{Aa}$	6	5	4	8		
	$N_{aa}$	6	3	3	3		
Absolute genotypic lineage rate of increase ( $R_{ab}$ )	$R_{AA}$	0.50	1.50	1.00		0.75	0.91
	$R_{Aa}$	0.83	0.80	2.00		1.33	1.10
	$R_{aa}$	0.50	1.00	1.00		0.50	0.79
Initial population size ( $N$ )		8	5	5	7		
Mean absolute rate of increase ( $\bar{R}$ )		0.63	1.00	1.40		0.88	0.96
Initial frequency of alleles derived from genotype $ab$ lineages ( $f_{ab}$ )	$f_{AA}$	0.25	0.20	0.30	0.21		
	$f_{Aa}$	0.38	0.50	0.40	0.57		
	$f_{aa}$	0.38	0.30	0.30	0.21		
Relative genotypic lineage rate of increase ( $r_{ab}$ )	$r_{AA}$	0.80	1.50	0.71		0.86	0.95
	$r_{Aa}$	1.33	0.80	1.43		1.52	1.15
	$r_{aa}$	0.80	1.00	0.71		0.57	0.83
Mean relative rate of increase ( $\bar{r}$ )		1.00	1.00	1.00		1.00	1.00



**Fig. 3** Schematic representation of a sexual population of diploid organisms over a period of three time units. The genotype at two loci is shown. Alleles are numbered with respect to the ancestor in the initial population ( $t = 0$ ) in which they are found. For calculations of representative rates of increase for this population, see Table 3



**Table 3** Representative rates of increase for the population of Fig. 3

Variable	Period ( $t$ to $t + 1$ )			Total/ 3 Gen	Mean/ Gen ( $G$ )
	0–1	1–2	2–3		
Absolute allelic rate of increase ( $R_{ia}$ ) (shown for ancestor 2 only)	$R_{2A}$	1.00	1.00	1.00	1.00
	$R_{2a}$	2.00	1.00	1.00	1.00
	$R_{2B}$	2.00	1.00	1.00	1.00
	$R_{2b}$	1.00	2.00	2.00	1.26
Absolute organismic lineage rate of increase ( $R_i$ ) (shown for ancestors 2 and 4)	$R_2$	1.50	1.00	1.25	1.08
	$R_4$	1.00	2.00	2.50	1.36
Initial number of alleles derived from genotype $ab$ lineages ( $N_{ab}$ )	$N_{AA}$	4	3	1	
	$N_{Aa}$	10	9	11	10
	$N_{aa}$	2	1	1	1
Absolute genotypic lineage rate of increase ( $R_{ab}$ )	$R_{AA}$	0.75	0.33	1.00	0.25
	$R_{Aa}$	0.90	1.22	0.91	1.00
	$R_{aa}$	0.50	1.00	1.00	0.50
Initial population size ( $N$ )	8	6.5	6.5	6	
Mean absolute rate of increase ( $\bar{R}$ )	0.81	1.00	0.92	0.75	0.91
Initial frequency of alleles derived from genotype $ab$ lineages ( $f_{ab}$ )	$f_{AA}$	0.25	0.23	0.08	0.08
	$f_{Aa}$	0.63	0.69	0.84	0.83
	$f_{aa}$	0.13	0.08	0.08	0.08
Relative genotypic lineage rate of increase ( $r_{ab}$ )	$r_{AA}$	0.93	0.33	1.09	0.33
	$r_{Aa}$	1.11	1.22	0.99	1.33
	$r_{aa}$	0.62	1.00	1.09	0.67
Mean relative rate of increase ( $\bar{r}$ )	1.00	1.00	1.00	1.00	1.00

population geneticists themselves there is little confusion about the *algebraic* meaning of fitness, at least as defined with reference to the discrete generation diploid model above. With respect to this model, it is clear that the fitness of an individual or group of individuals corresponds respectively to the individual or average rate of increase over a single generation (= mean number of successful gametes/2).

Yet this algebraic equivalence does not at all capture the intended meaning of “fitness,” which (at least when authors are being careful) is always defined not as the *average* rate of increase of a group of lineages (of a given genotype) but as the *expected* rate of increase. This allows for the possibility that “accidents” in any particular population (“genetic drift”) may make the average different from the ideal or expected quantity.

The difference between the average and the expected rate of increase brings up a fundamental issue in the study of differential lineage survival (“natural selection”)—the distinction between a *descriptive* and a *causal* analysis. All of the measures arrived at above for rate of increase are merely descriptive; they tell us absolutely nothing about the causes of differential increase among various lineages.

In fact, until now I have been dealing with genetics only in terms of gene transmission, not gene expression. Yet in order to say something about the *causes* of differential increase of genetic lineages, it is necessary to treat the rate of increase of each lineage as some function of its *effects* on the external world. The challenge then becomes the definition of such a function.

The simplest assumption would be that each of the alleles at a locus has a constant effect, which completely determines its own expected rate of increase, independent of the circumstances it is in. If we call the total of these circumstances the “environment,” then we can write:  $E(R_a) = F(a, \text{environment}) = F(a) = C$ , where  $C$  is a constant, and  $E$  denotes the expectation, or the average across an infinite series of trials. Of course such a model is extremely unrealistic for any allele, except perhaps a dominant lethal. In particular, this constant allelic fitness model immediately runs up against a basic fact of Mendelian inheritance in diploid organisms—alleles are always present in pairs, which may interact in their effects (dominance). In other words, the genetic environment of an allele, even at a single locus, is often an important determinant of the effects of that allele.

A slightly more realistic model would be one in which single (or multiple) locus *genotypes* are considered to have constant effects, completely determining their own expected rate of increase:  $E(R_{ab}) = F(ab, \text{environment}) = C$ . It is this model of constant fitness of single locus genotypes that is at the heart of the standard approach to population genetics (e.g., Hartl & Clark, 1997; Hedrick, 2000),

although much more complicated models have of course been developed.

It is important to remember that when this model is used one is treating the rate of increase not only of the genetic lineages at that particular locus, but of *all lineages* carried by that organism, as determined (at least probabilistically) by the genotype at that locus. Yet it is obvious that the rate of increase of genetic lineages in organisms of a particular genotypic class depends on more than just that genotype. All of these other factors are lumped together as “environment.”

The “environment” thus includes, among other things, the genotype at all loci not considered, the phenotype of the organism from conception to death, the phenotypes of other members of the population, and the characteristics of the physical and biological environment. When one assumes constant fitnesses, one usually implicitly assumes that the genotype at other loci is irrelevant, the phenotype of the organism is constant (since it is determined by the genotype), the phenotypes of other members of the population are irrelevant, and the characteristics of the physical and biological environment are constant.

Let us also assume that mating is random with respect to the locus under consideration, so that each generation new genotypes are formed with expected frequency  $E(f_{ab}) = f_a f_b$  (Hardy–Weinberg proportions), where  $f_{ab}$  is the frequency of the *ordered* genotype  $ab$ , and  $E(f_{ab}) = E(f_{ba})$ . Define a variable for fitness,  $W_{ab} = E(R_{ab})$ . As for frequencies,  $E(R_{ab}) = E(R_{ba})$ , so  $W_{ab} = W_{ba}$ . If we further assume population size to be infinite, the actual values,  $R_{ab}$  and  $f_{ab}$ , will equal the expected values,  $W_{ab}$  and  $f_a f_b$ , and we need not take random effects into account.

With these assumptions, one can construct a simple, familiar model of evolutionary change at a single locus due to differences in genotypic fitness. For the alternative alleles  $A$  and  $a$  with frequencies  $p$  and  $q$  ( $= 1-p$ ) we have:

Zygote	Frequency	Fitness
$AA$	$p^2$	$W_{AA}$
$Aa$	$2pq$	$W_{Aa}$
$aa$	$q^2$	$W_{aa}$

and the mean fitness  $\bar{W} = \sum f_{ab} W_{ab} = p^2 W_{AA} + 2pq W_{Aa} + q^2 W_{aa}$

In order to calculate the frequencies of genotypes in the next generation of zygotes, it is necessary to find the new gene frequencies,  $p'$  and  $q'$ . We have:

$$p' = (p^2 W_{AA} + pq W_{Aa}) / \bar{W} = p(p W_{AA} + q W_{Aa}) / \bar{W}$$

$$q' = (q^2 W_{aa} + pq W_{Aa}) / \bar{W} = q(q W_{aa} + p W_{Aa}) / \bar{W}$$

As we have seen above in our discussion of rates of increase, division of the absolute fitnesses by  $\bar{W}$ , the mean

fitness in the population, is required for the new allelic frequencies to sum to unity.

Differential fitness at a single locus has only three possible forms under these circumstances: “directional selection” ( $W_{AA} > W_{Aa} > W_{aa}$  or  $W_{AA} < W_{Aa} < W_{aa}$ ), “overdominance” ( $W_{AA} < W_{Aa} > W_{aa}$ ), or “underdominance” ( $W_{AA} > W_{Aa} < W_{aa}$ ). At equilibrium,  $p' = p$ , so  $\bar{W}$  is a constant, and  $\Delta\bar{W} = 0$ . As it turns out,  $\bar{W}$  is at a maximum for stable equilibrium (overdominance) and a minimum for unstable equilibrium (underdominance), so that  $\Delta\bar{W}$  is always positive under this system of evolution. In other words, in this model, as gene frequencies change under natural selection, *mean fitness of the population always increases*. Nevertheless, there is no guarantee that the population will evolve to the highest possible mean fitness, for in the case of underdominance, the homozygote with the lower fitness is nevertheless favored when it is common.

### Ironing Out Wright’s “Surface of Selective Value”

In the one locus, constant genotypic fitness, random mating, infinite population size model we are considering, mean fitness always increases, and stable equilibria are local peaks of mean fitness in the field of gene frequencies. Thus one can imagine the population at any time as either sitting on or evolving toward such a peak (Fig. 4A).

As noted in the introduction, this image of evolution is closely tied to Sewall Wright’s (e.g., 1932, 1988) vision of a “surface of selective value” or adaptive landscape on which the population evolves. In fact, the algebraic form of the equations we have been using derives directly from Wright, including the use of  $W$  for fitness values (Wright, 1937). In most current textbooks this connection is explicit, and an adaptive landscape is defined as a “graph of mean population fitness ( $\bar{w}$ ) against gene frequency” (Ridley, 2004, p. 214) or a “surface of mean fitness for all possible combinations of allelic frequency” (Griffiths et al., 2005, p. 686). Twenty years ago Futuyma (1986, p. 172) noted that the adaptive landscape is “perhaps the most popular metaphor for evolutionary change” and in his recent book he noted that the metaphor is still “widely used in evolutionary biology” (Futuyma, 2005, p. 287). It is rather disconcerting to find, then, that there are fundamental problems in interpreting Wright’s metaphor in these terms.

First of all, since this metaphor requires that mean fitness increase in time, and mean fitness is just expected population growth rate, population growth rate must continually increase. Yet the image of a constantly increasing population growth rate hardly corresponds to any reasonable view of the normal evolution of a population. The problem obviously lies in our assumption that fitnesses of

genotypes at a single locus are constant, and independent of environment. In any natural situation one would of course expect absolute fitnesses to at least eventually decrease as the population increases in number, even allowing other aspects of the “environment” to remain constant.

But if it is obviously absurd to consider absolute fitnesses as constant, it is perhaps not so absurd to think that for some loci, the *ratios* of the fitnesses of the different genotypes might be constant over time. Since we are only dealing with changes in allele *frequencies*, not numbers, the fitness ratios completely determine the evolution of the population in this model, and there is no need to use absolute fitnesses. If we only care about fitness ratios, we can scale the fitnesses however we please; most commonly (again following Wright), the genotype with the highest fitness is given the fitness value of unity, and all other genotypes are scaled relative to this (Fig. 4B). These rescaled absolute fitnesses are known as “relative fitnesses” (the reason for the quotation marks will be clear in a moment). With this rescaling, one can now regard the adaptive landscape as a landscape of mean “relative fitness.” This is of course the interpretation used in the textbooks quoted above.

Yet there is now another problem in the interpretation of the metaphor: what is the meaning of differences in mean “relative fitness” among populations? If mean fitness is not (expected) population growth rate, what is it? These questions are particularly important since a major theme of Wright’s shifting-balance theory of evolution is that selection alone may cause a population to get stuck on a low adaptive peak, with genetic drift (due to small population size and inbreeding in local populations) necessary for a population to cross the adaptive valley to a neighboring, higher peak. This was stated very clearly by Wright in his first discussion of the surface of selective value (Wright, 1932, pp. 163–164): “The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field.”

Unfortunately, it turns out that in terms of the model we are using, *the mean “relative fitness” of a population has no meaning whatsoever*. Because one is dividing the absolute fitnesses by an arbitrary value, the mean fitness of a population itself is entirely arbitrary. This is clearly recognized by most population geneticists and evolutionary biologists, although they do not usually state this as emphatically as I have. Instead, they just caution against trying to compare the mean “relative fitnesses” of different populations. For example, Griffiths et al. (2005, p. 633) state:

“This maximization of fitness does not necessarily lead to any optimal property for the species as a

whole because fitnesses are only defined relative to each other within a population”

and Hartl and Clark (1997, p. 230) note:

“...  $\bar{w}$  is the average fitness *in* the population, not the average fitness *of* the population.”

If this is true then what can these authors mean by employing the metaphor of the adaptive landscape? If the height of a population’s adaptive peak means nothing, then why be concerned about whether a population is able to reach a higher peak, by genetic drift or otherwise?

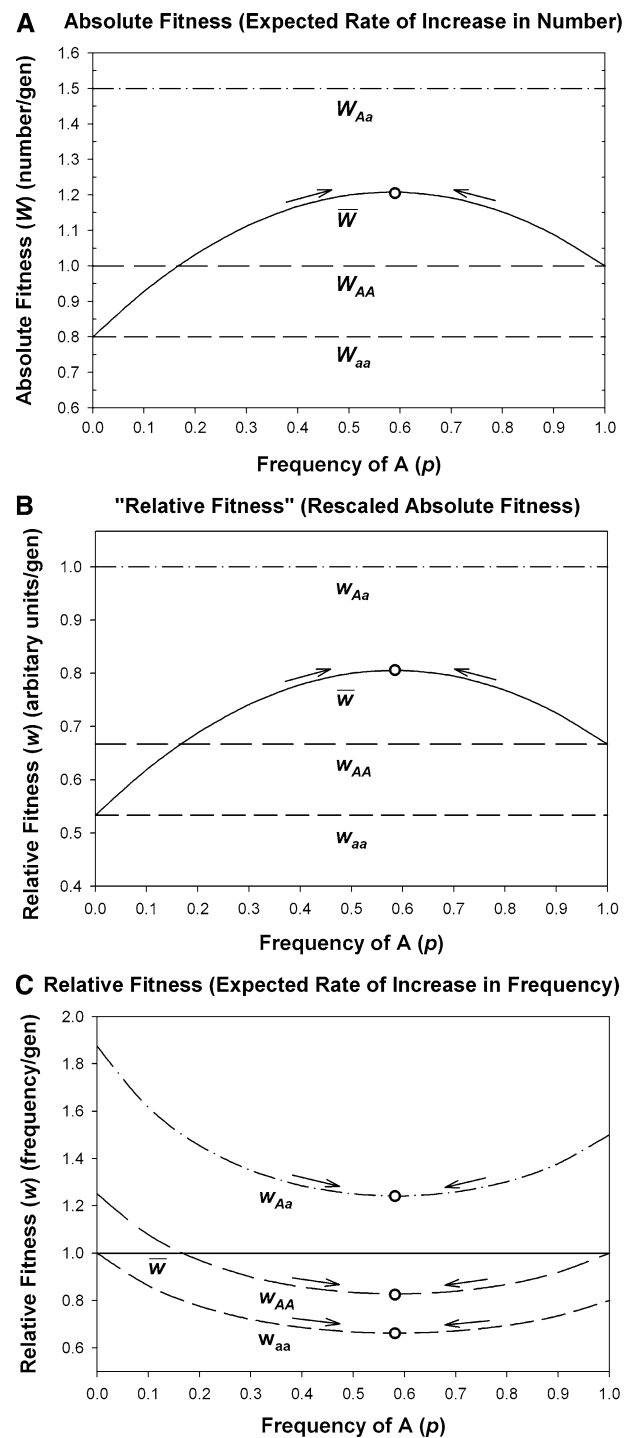
I believe that the persistent popularity of Wright’s metaphor of the adaptive landscape, in spite of the fact that a critical examination shows it to make no sense whatsoever (Gayon, 1998; Provine, 1986), is the result of a persistent confusion between relative and absolute fitness. This confusion comes from the belief that these quantities somehow are different measures of the same thing. If relative fitnesses are to be truly relative, they must be relative to the situation of the population as a whole. Instead “relative fitnesses,” as commonly used, are no more than conveniently rescaled absolute fitnesses. The arbitrary nature of the scaling is reflected in the arbitrariness of  $\bar{w}$ , which is essentially a dummy variable expressing one’s choice of scaling. This can be seen quite clearly in a comparison of Fig. 4A, B.

I have so far neglected to compare “relative fitnesses” with relative rates of increase. Relative rates of increase [as defined in Eqs. 5–8 above], unlike “relative fitnesses” under the standard definition, are *not* arbitrary values. Instead, they express the rate of increase or decrease in frequency per generation. Similarly, we can define *standardized* relative fitnesses in terms of relative rates of increase, such that  $w_{ab} = E(r_{ab})$ . Under this definition for all periods  $\bar{w} = 1$  and the familiar equations above become:

$$p' = (p^2 w_{AA} + pq w_{Aa}) = p(pw_{AA} + qw_{Aa})$$

$$q' = (q^2 w_{aa} + pq w_{Aa}) = q(qw_{aa} + pw_{Aa})$$

Recognizing that under this model the rate of increase (“marginal fitness”) of the A allele is given by  $w_A = (pw_{AA} + qw_{Aa})$ , we have simply  $p' = pw_A$ , making the relation between changes in gene frequency and relative fitness quite clear. Of course the simpler form of these equations comes at a price: if gene frequencies are changing, the genotypic fitnesses can no longer be constant; in other word, standardized relative fitnesses are necessarily frequency dependent. In terms of absolute fitnesses the (standardized) relative fitness  $w_{ab} = W_{ab}/\bar{W}$ . Since mean absolute fitness ( $\bar{W}$ ) increases under natural selection in this model, the relative fitness of each



**Fig. 4** Comparison of an “adaptive landscape” for absolute fitness (A) with those for two different representations of “relative fitness”: rescaled absolute fitness, with the maximum genotypic fitness at 1.0 (B), and standardized relative fitness, with mean fitness at 1.0 (C). The model used is a simple case of overdominance at a single locus in an infinite, random-mating population, with absolute fitnesses  $W_{AA} = 1.0$ ,  $W_{Aa} = 1.5$ ,  $W_{aa} = 0.8$

genotype must decline. In fact, with this definition, a population is at a stable equilibrium when the relative fitness of each genotype is at a minimum (Fig. 4C). This

point is thus a *joint minimum of relative fitness* for all genotypes.

I believe that the use of standardized relative fitnesses (Fig. 4C), while unfamiliar, is much less prone to misinterpretation than the use of “relative fitnesses” that are merely rescaled absolute fitnesses (Fig. 4B), since standardized relative fitnesses have the explicit meaning of expected rate of increase in frequency, rather than being values on an arbitrary scale. A genotype with a standardized relative fitness greater than one is leaving greater than the average number of descendants. Currently, students are told that “...selection can also be described as a process that *increases mean fitness*” (Griffiths et al., 2005, p. 633), which seems to say something real about the effects of selection. Lest they get too confident, however, they are immediately warned that “It is relative (not absolute) fitness that is increased by selection.” It is almost unavoidable that such a nebulous concept of relative fitness should acquire some of the associations more proper to absolute fitness.

Some readers may see a problem with the use of standardized relative fitnesses in the fact that they cannot remain constant while allele frequencies change. However there is no reason to expect that *relative fitnesses* should be constant, just because *fitness ratios* are constant. No one objects to the fact that the marginal fitnesses of alleles are not constant with constant genotypic fitnesses. The situation here is somewhat similar. Standardizing the dummy variable  $\bar{w}$  at unity simply makes it mathematically impossible for the (standardized) relative fitnesses of genotypes to remain constant as gene frequencies change.

Importantly, under the now usual definition of “relative fitnesses” as rescaled absolute fitnesses (Fig. 4B), this necessity for change in their values as frequencies change is concealed by the practice of “normalizing” genotypic frequencies after selection by the factor  $\bar{w}$  (see above). Unfortunately, the effect of this normalization is often overlooked. Wallace (1991), in an extremely interesting review of the genetic load controversy, concludes that Haldane’s (1957) calculations on the “cost of selection” were entirely erroneous, due to his adoption of the “arbitrary convention that the maximum, or optimal, fitness shall be assigned the value of 1.00” (p. 76). He attributes this error to Haldane’s “failure to realize that normalization of the population to 100% while maintaining a constant population size resurrected most ‘dead’ individuals from the category designated ‘selective deaths’” (p. 77). If Haldane, Crow, Muller, and many other prominent geneticists could be misled by the standard convention into calculating figures for genetic load which have “little to do with fitness as measured by the ratio of daughters to mothers” (Wallace, 1991, p. 135), it is perhaps not unreasonable to think that evolutionary biology would be

better served by the use of standardized relative fitnesses, as proposed here.

Wallace in fact proposes a similar redefinition himself (though he is thinking of absolute fitness with constant population size): “If the value 1.00 is assigned to  $\bar{W}$  rather than to the genotype with the maximum or optimum fitness, the *relative* [i.e., ratios of] Darwinian fitnesses of different genotypes remain unchanged—only the numerical values assigned to them are altered” (1991, p. 134).

What becomes of the adaptive landscape if one uses standardized relative fitnesses rather than traditional “relative fitnesses” (rescaled absolute fitnesses)? If the adaptive landscape is regarded as the surface of  $\bar{w}$  then its form becomes quite simple: it is a flat plane at  $\bar{w} = 1$  (Fig. 4C; this was recognized by Wright himself at various times, e.g., 1949, p. 376). I do not imagine that such a metaphor of the adaptive landscape would have ever gained much popularity. Alternatively, one could have a landscape measured in terms of the relative fitness of any one of the genotypes: stable points would be adaptive pits, barriers adaptive ridges (Fig. 4C). A landscape based on the variance in allelic (marginal) fitness would show both stable and unstable equilibria as pits of height zero.

The question of pits or peaks, however, is not important. What is important is that in none of these alternative cases is there any reason to consider the movement from one adaptive peak (or pit) to another progressive, as suggested by Wright’s metaphor of “the movement from lower to higher peaks in such a field.” There is thus no “problem” of being stuck on a low peak (or in a shallow pit) for a population to overcome, by genetic drift or otherwise.

But was Wright really so dangerously misled by his metaphor? Is there something else he might have meant other than the interpretation given above, which would allow us to make sense of his conception of the adaptive landscape? To answer this, we must turn to a short history of the concept. This history is especially important for elucidating Wright’s concept of fitness. Moreover, it will prepare the way for a comparison with R. A. Fisher’s view of fitness, as incorporated in his “Fundamental Theorem of Natural Selection.” Only by understanding the historical roots of our current concept of fitness, as developed by these two pioneers of population genetics, can we hope to clarify the role of fitness in evolutionary theory.

### The Genesis of Wright’s “Surface of Selective Value”

In his excellent scientific biography of Wright, Provine noted that “Despite its great attractiveness and apparent ease of interpretation, the surface of selective value is one of Wright’s most confusing and misunderstood contributions to evolutionary biology” (1986, p. 308). In an



extensive discussion (pp. 307–317), Provine showed that at least three fundamentally irreconcilable concepts of this surface have been used in evolutionary biology, two of them by Wright himself.

The second of these surfaces is the one we have been considering: *mean fitness of the population* plotted as a function of *allele frequencies*. A third type of surface was introduced by Simpson (1944), with *mean fitness of individuals* plotted as a function of their *phenotype* (this surface has had some recent support; see Arnold, 2003; Arnold et al., 2001). Provine showed that neither of these corresponds to the concept of the surface first proposed by Wright (1932), in which the *mean fitness of genotypes* is plotted as a function of those *genotypes* (see also the detailed discussion in Gayon (1998), Gavrillets (2004)).

Wright's 1932 paper was prepared as a nontechnical summary of the results of his mathematical analysis of "Evolution in Mendelian Populations," published the preceding year (see Provine, 1986, pp. 283–287; Wright, 1986 reprints all of his earlier papers I will be discussing in detail). He began by stressing the immense genetic diversity provided by the Mendelian mechanism: "With 10 allelomorphs at each of 1000 loci, the number of possible combinations is  $10^{1000}$  which is a very large number" (p. 356). (Though Wright does not point this out, this figure represents only the number of homozygous combinations). Nevertheless,

...not all of this field is easily available in an interbreeding population. Suppose that each type gene is manifested in 99 percent of the individuals.... The average individual will show the effects of 1 percent of the 1000, or 10 deviations from type, and...only a small proportion will exhibit more than 20 deviations from type.... The population is thus confined to an infinitesimal portion of the field of possible gene combinations, yet this portion includes some  $10^{40}$  homozygous combinations....

He then introduced the surface of selective values: "If the entire field of possible gene combinations be graded with respect to adaptive value under a particular set of conditions, what would be its nature?" (p. 357). Here adaptive values (fitnesses) are being assigned to individual multilocus *genotypes* within the entire field of possible genotypes. His figure 1 (here Fig. 5) illustrates this field for "combinations of from 2 to 5 paired allelomorphs."

Interestingly, this figure again represents only the homozygotes, with each homozygous genotype being connected to all others differing at only a single locus. Thus "in the last case, each of the 32 homozygous combinations is at one remove from 5 others...."

The reason for Wright's focus on homozygotes is clear if we remember his calculations above; at the time he,

along with other geneticists, expected the majority of loci in the average individual to be homozygous for the "type" allele, with only a few heterozygous or homozygous for a rare allele. In this case, most individual genotypes would be close to the multiply homozygous (+) or "type" genotype in the field of gene combinations. Alternative states of the population would involve high frequencies of one of the alternative alleles, with most genotypes now close to this alternative homozygous type.

Wright now goes on:

The 32 combinations here compare with  $10^{1000}$  in a species with 1000 loci each represented by 10 allelomorphs.... The two dimensions of figure 2 [here Fig. 6] are a very inadequate representation of such a field. The contour lines are intended to represent the scale of adaptive value.

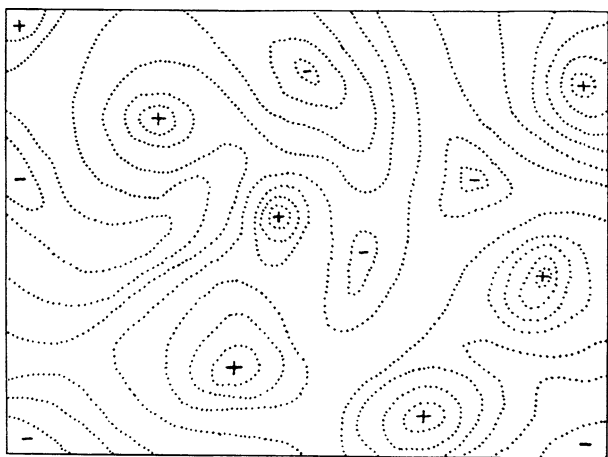
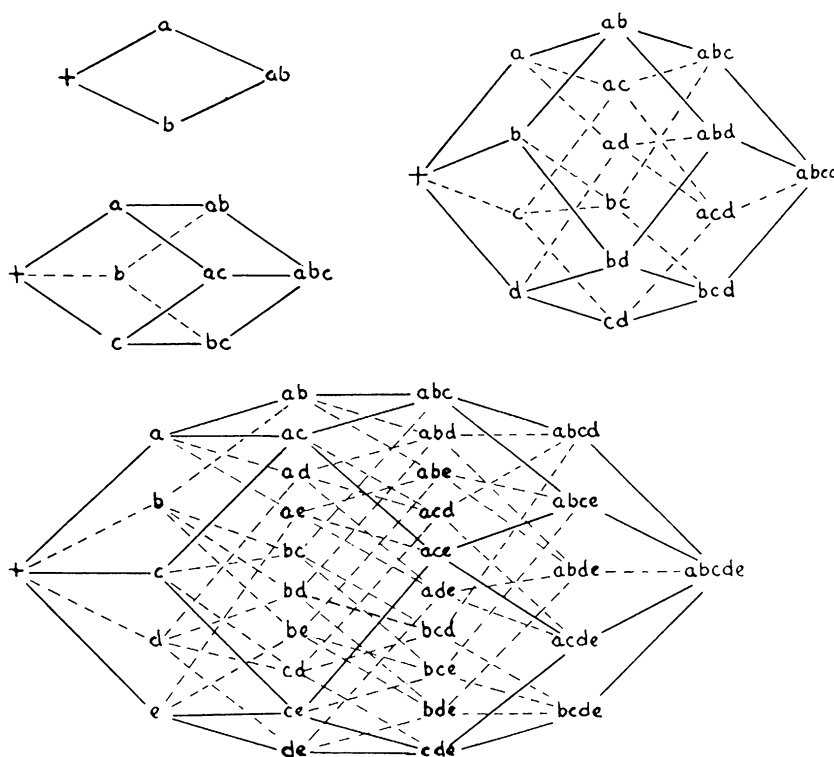
One possibility is that a particular combination gives maximum adaptation and that the adaptiveness of the other combinations falls off more or less regularly according to the number of removes. A species whose individuals are clustered about some combination other than the highest would move up the steepest gradient toward the peak, having reached which it would remain unchanged except for the rare occurrence of new favorable mutations.

But even in the two factor case (figure 1) it is possible that there may be two peaks, and the chance that this may be the case greatly increases with each additional locus. With something like  $10^{1000}$  possibilities (figure 2) it may be taken as certain that there will be an enormous number of widely separated harmonious combinations. The chance that a random combination is as adaptive as those characteristic of the species may be as low as  $10^{-100}$  and still leave room for  $10^{800}$  separate peaks, each surrounded by  $10^{100}$  more or less similar combinations. In a rugged field of this character, selection will easily carry the species to the nearest peak, but there may be innumerable other peaks which are higher but which are separated by "valleys." The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field. In order that this may occur, there must be some trial and error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies. To evolve, the species must not be under strict control of natural selection. (pp. 358–359)

I have quoted rather fully from this manuscript so that there should be no confusion as to Wright's meaning. It is clear that in this initial version, each adaptive peak is in fact a



**Fig. 5** Figure 1 of Wright (1932). “The combinations of from 2 to 5 allelomorphs.” The figure shows the homozygous combinations possible, with each genotype connected to those differing by only a single gene replacement



**Fig. 6** Figure 2 of Wright (1932). “Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect to adaptive-ness.” This is the first published representation of the adaptive landscape

cluster of genotypes. The top of the peak (represented by a + in both Figs. 5, 6) represents the favored homozygous “type” genotype, which is surrounded by genotypes that decrease in adaptive value as they get further and further away from the favored type (in terms of gene replacements). By positing the existence of adaptive peaks other than the one currently occupied, Wright was arguing that there might be many multilocus homozygous genotypes

with high adaptive value that are extremely unlikely to occur in a large, random breeding population. With “many small local races, each breeding largely within itself but occasionally crossbreeding,” however, a number of non-“type” alleles could become common in a race, causing one of the other favored multiply homozygous genotypes to occur with high frequency. Thus Wright concludes that “with many local races, each spreading over a considerable field and moving relatively rapidly in the more general field about the controlling peak, the chances are good that one at least will come under the influence of another peak.”

So far so good. Yet Wright goes on: “If a higher peak, this race will expand in numbers and by crossbreeding with others will pull the whole species toward the new position. The average adaptedness of the species thus advances under intergroup selection, an enormously more effective process than intragroup selection.” Unfortunately, even in this initial version of the adaptive landscape Wright does not indicate what it might mean for a species to move to a higher peak and increase in adaptedness (though the expansion phase would certainly be tied to a temporary increase in mean absolute fitness of the expanding race). As with the standard gene frequency based surface discussed above, it is not at all clear on what scale adaptive value is to be measured.

To understand what Wright had in mind, it is necessary to understand that, in Provine’s words (1986, p. 1), “Wright’s shifting-balance theory of evolution in nature

grew directly out of his theory of evolution in domestic breeds” (see also Gayon, 1998). Wright himself was quite aware of this: in his autobiographical 1978 paper on “The relation of livestock breeding to theories of evolution,” he recalls that

It was apparent...from my studies of the breeding history of Shorthorn cattle that their improvement had actually occurred essentially by the shifting balance process rather than by mere mass selection. There were always many herds at any given time, but only a few were perceived to be distinctly superior.... These herds successively made over the species by being principal sources of sires. (pp. 1198–1199)

Wright seems never to have realized that while in the context of domestic breeds it may be reasonable to speak of “improvement” by selection of “superior” herds, where the standard of value is determined by the goals of the breeder, no such *a priori* standard of overall value exists in nature.

In fact, by focusing on the hypothetical ways in which organisms could evolve toward a future state of improved adaptation, Wright introduced a teleological element into his evolutionary theory. The underlying pattern of thinking has been outlined in the introduction: the current state of the population is conceived of as maladapted with reference to some potential future state (a higher “adaptive peak”), with natural selection then acting as a force to drive the population towards the more adapted state (aided by genetic drift in the initial crossing of the valley).

This teleological element was easy for Wright to overlook in 1932, due to the metaphorical way in which he presented his shifting balance theory. Yet as Provine (1986, p. 207) perceptively notes, “One of Wright’s lifelong tasks was to bring his quantitative theory of evolution closer to his qualitative theory.” It is both fascinating and instructive to trace the path by which Wright later linked his metaphorical version of the surface of selective values to the mathematically defined measure of average fitness,  $\bar{w}$ . As we shall see, it was essentially confusion between improvement in single features and improvement in general that allowed him to make this connection.

The first step was taken by Wright in a pair of 1935 papers (1935a, b), originally written as one (Wright, 1986, pp. 207–208). Here he examined the situation in which the quantitative grade of a character on a primary scale depends on the constant effects of alternate alleles at many independent loci, with the optimum grade of the character (in terms of fitness) being intermediate. He then introduced a secondary scale measuring fitness, based on the squared deviation of the actual value of each individual ( $S$ ) from the optimum value ( $O$ ). This scale was expressed by the variable  $H = -(S - O)^2$ ; thus  $H$  is at its maximum of 0 for

individuals in which the character is at its optimum grade, and falls off symmetrically for character values on either side of the optimum. Wright’s basic assumption, that it is “often the case that the best adapted individuals are those nearest the average in every respect,” (1935a, p. 243) was not unreasonable. But Wright went well beyond this assumption, treating the optimum value as a fixed goal toward which the population would evolve (if able to), and with reference to which its average adaptive value could be compared.

In the first paper (1935a), Wright determined the mean and variance of  $H$  for any set of gene frequencies, analyzed the variation in  $H$  between genotypes into additive, dominance, and epistatic components, and calculated correlations in  $H$  between relatives. In the second paper (1935b), he extended this approach to consider “Evolution in populations in approximate equilibrium.” Here he first introduced the gene frequency version of the adaptive landscape:

The nature of the evolutionary processes under the conditions described may be visualized by treating the population at a given moment as located at a point in a multidimensional space defined by the set of gene frequencies ( $q_1, \dots, q_n$ ) pertaining to the *plus* members ( $A_1, \dots, A_n$ ) of gene pairs affecting the character (cf. Haldane, 1931). Ordinates are to be erected measuring the average adaptive value ( $\bar{H}$ ) of the character. The signs of  $\bar{H}$  and  $\gamma_i$  (net effect of substitution of  $A_i$  for  $a_i$  on adaptive value in the population in question) are taken so as to make the high points correspond to optimal values. (p. 257)

Provine (1986, p. 312) asks “how and when did Wright get the idea for this new conception of the surface of selective values?” From the passage just quoted, he considered the obvious answer to be “from Haldane’s 1931 paper on ‘metastable populations,’ where Haldane envisioned a population with  $m$  genes as being situated on a hypercube of  $m$  dimensions.” Provine rejects this possibility, however, based on Wright’s first known mention of the adaptive landscape, in a 1931 letter to R. A. Fisher. Here Wright asked Fisher to “Think of a field of visible joint frequencies of all genes as spread out in a multidimensional space. Add another dimension measuring degree of fitness.” Provine shows that Wright subsequently shifted back and forth between the two conceptions as was convenient, without clearly distinguishing between them. In a 1988 paper Wright responded to Provine’s criticisms by arguing that Provine “was looking for something more mathematical than was intended” by the metaphor (p. 115). He went on to recap the individual genotype version of the landscape, without ever addressing the gene frequency version (for an interpretation more sympathetic to Wright,

see Crow, 1990). With this rather lengthy aside, we may now return to the second 1935 paper.

Whereas in the first paper Wright had calculated  $\bar{H}$  and  $\partial\bar{H}/\partial q_i = 2\gamma_i$  purely formally, as they pertained to the population at a given time (as was necessary to partition genetic variance and calculate correlations among relatives), here he treated these same quantities as pertaining to the dynamic evolution of the population:

The rate of change of gene frequency per generation in the case of no dominance is well known to be  $\Delta q = sq(1 - q)$ , where  $s$  measures the selective disadvantage of one allelomorph (Fisher, 1922). In the general case, the selective disadvantage must be proportional to the momentary net effect of gene replacement on adaptive value

$$\Delta q_i = s\gamma_i q_i(1 - q_i). \quad (4)$$

The rate of change of the mean adaptive level of the population per generation can be written

$$\Delta\bar{H} = \sum_{i=1}^n \frac{\partial\bar{H}}{\partial q_i} \Delta q_i = 2s \sum \gamma^2 q(1 - q). \quad (5)$$

Let us be quite clear on what Wright was doing here. His assumptions of independence of loci and random mating allowed him to treat the distribution of genotypes as a function of allele frequencies. His assumption of constant allelic effects then allowed him to treat the distribution of phenotypes as a function of allele frequencies. Finally, the assumption of constant fitness of phenotypes (which is appropriate only if expected rate of increase depends exclusively on the quantitative value of this single character) then allowed him to treat the mean fitness of the population,  $\bar{H}$ , as a function of the allele frequencies.

Due to these assumptions, Wright was able to derive the average effect on the fitness of an individual of a given allelic substitution ( $\gamma_i$ ) as the partial derivative of mean fitness with respect to change in frequency of that allele, and was then able to consider the *rate of change in frequency* of the allele to be determined by this effect on fitness (as modified by the frequency factor  $q(1-q)$ ), or in other words by the slope of the “surface” of  $\bar{H}$  along the axis of allele frequency. Summing the rate of change in frequency times the effect of change in frequency on fitness over all loci then gave the rate of increase in mean fitness of the population as a whole.

Strangely, this whole section of the paper, which contains the crux of the connection between the static effects of alleles and the dynamic evolutionary change of their frequency, is both rather sloppy and vague. Thus Wright cites Fisher (1922) for the “well known” formula for rate

of change in gene frequency per generation, even though Fisher had used the differential form  $dp/dT = pq\alpha$  (where  $\alpha = \ln(1 - s)$  in Wright’s terminology). Moreover, the discrete generation form given by Wright, corresponding to the situation in which alternative alleles with frequencies  $q$  and  $(1-q)$  reproduce in the ratio  $1:(1-s)$  per generation, is actually only the approximation for  $s \ll 1$  (Wright, 1931). The full form is instead  $\Delta q = sq(1 - q)/[1 - s(1 - q)]$ , in which the denominator corresponds to what he would later call  $\bar{w}$ .

Most importantly, the inclusion of the factor  $s$  in Wright’s Eqs. 4 and 5 is puzzling, since nowhere in either paper does he explicitly define this factor. It is clearly not the same  $s$  as that in the equation  $\Delta q = sq(1 - q)$ , because  $\gamma_i$  must enter into that  $s$ . Instead it is an arbitrary constant of proportionality, corresponding to the phrase “must be proportional to” (cf. also Wright, 1935a, p. 249). In fact, we have seen that this factor cannot be a constant at all if the distribution of genotypes is changing, since to be accurate it must incorporate the expression  $1/\bar{w}$ . The inclusion of the undefined factor  $s$  makes his equation 4 rather unhelpful for calculating the actual rate of change in frequency of any allele. In fact, by failing to explicitly define  $s$ , Wright left the connection between adaptive value, defined in terms of  $H$ , and allelic fitness (expected rate of increase), defined by the rate of change in gene frequency, entirely nebulous. This is in fact exactly the same problem bequeathed to us in the common definition of relative fitnesses, as detailed above.

In the conclusion to this paper, Wright noted that in the model he was considering “all of these peaks must be at the same or very nearly the same level, and even if the locus of the population could by some means be moved across a saddle to a new peak it would by no means advance” (Wright, 1935b, p. 263). Yet he reassured himself that

The subject presents a somewhat different aspect when we recall that genes in general have multiple effects. The system of peaks relative to one character is not independent of that relative to another. Moreover, it is the harmonious adjustment of all characteristics of the organism as a whole that is the object of selection, not the separate metrical ‘characters.’ ...it seems safe to postulate an inconceivably great number of ‘peaks,’ many of them characterized by different harmonious combinations of characters.... These may be at all levels and of all orders of dominance and subordination in relation to each other. It has seemed to me (1929 *et seq.*) that the central problem of evolution (as of live stock improvement (Wright, 1920, 1922)) is that of a trial and error mechanism by which the locus of a population may be carried across a saddle from one peak to another

and perhaps higher one. ...The mathematical analysis in the present paper deals with a case in which there may be innumerable separate peaks though all at approximately the same level. It may be looked upon as a simplified model of the complex case in which adaptation of the organism as a whole replaces that of a single metrical character. (p. 264)

It is again clear from this passage that Wright's perspective on evolution was fundamentally that of a breeder, intent on the improvement of his stock. His job as a breeder was to solve the problem of a population failing to respond to selection, or responding too slowly, and he assumed that evolution in nature was faced with a similar problem. The metaphor of peaks of different levels was thus for him an a priori necessity, expressing the different levels of potential improvement one could aim for. Although in this case his mathematical model failed to provide much support for this image, he felt safe in concluding that when complicating factors were taken into account, his general picture of evolution would certainly be upheld.

The final step toward the mathematization of his metaphor was taken by Wright (1937), when he first introduced the variable  $w$  to refer to the fitness of a genotype. Wright clearly had in mind not the absolute fitness, but the "relative fitness" of each genotype: "The selective value of zygotes (relative to a certain standard) will be designated  $w$  and the mean value for a population,  $\bar{w}$ " (Wright, 1937, p. 307).

In this paper, Wright began by showing that for the classical model of one locus with two alleles under random mating

$$\Delta q = \frac{q(1-q)}{2\bar{w}} \frac{d\bar{w}}{dq}.$$

Wright was justifiably unsatisfied with considering a single locus to be the sole determinant of fitness, however, since

...more generally, selective values depend on the interaction of the entire system of genes. It is the harmonious development of all characteristics that determines the success of an organism, not the absolute grades of separate elementary characters, and still less its composition with respect to a single series of alleles. A gene that is favorable in one combination may be deleterious in another. However, if values of  $w$  are assigned to each possible combination, the rate of change of the frequency of a particular gene under selection (with specified values of all other gene frequencies) is given by the formula

$$\Delta q_i = \frac{q_i(1-q_i)}{2\bar{w}} \frac{\partial \bar{w}}{\partial q_i}. \quad (\text{pp. 309-310}).$$

Note that, as in the earlier paper, Wright assumed constant fitnesses. However the fitnesses are now assigned to complete multilocus genotypes (as in the 1932 paper), rather than to "the absolute grade of separate elementary characters." This certainly seems somewhat more reasonable, as one can then refer these constant fitnesses of genotypes to a constant external environment. Nonetheless, there remained two major problems with his approach (Edwards, 2000).

First, it is important to remember that in order to take the partial derivative of  $\bar{w}$  with respect to change in allele frequency,  $\bar{w}$  must be a function of allele frequency, and thus the distribution of *genotypes* on which  $\bar{w}$  depends must also be a function of allele frequency. For this to be true, not only must one assume random mating and independence of loci (no linkage), but one must assume an infinitely large population in which each of these genotypes can occur with its proper frequency, since "there is no reasonable chance that any two individuals have exactly the same genetic constitution in a species of millions of millions of individuals persisting over millions of generations" (Wright, 1932, p. 356). The appearance of increased realism in this new definition is therefore illusory.

Nevertheless, because he again made the same simplifying assumptions he had made in the earlier papers (1935a, 1935b), Wright was again able to treat the *rate of change in frequency* of the allele as determined by the *effect* of this allelic substitution on average fitness, or in other words by the slope of the "surface" of  $\bar{w}$  along the axis of allele frequency.

This brings up the second and even more serious problem: the meaning of  $\bar{w}$ , the average "relative fitness" of the population. As we have already seen, the mean "relative fitness" of the population is essentially a dummy variable, created by holding "relative fitnesses" constant when there is genetic change occurring in the population. By contrast, if one instead uses  $W$ 's, or absolute fitnesses,  $\bar{W}$  has the explicit meaning of population growth rate. Under such a definition, however, one must acknowledge the artificiality of the assumptions made by Wright, which lead to the absurd conclusion that evolution will in general involve a constantly increasing population growth rate. There is simply no other alternative, given the models Wright was using. Thus in answer to the question posed at the end of the last section, it is clear that Wright was in fact seriously misled by his metaphor. The resulting confusion between absolute and relative fitnesses was bequeathed to us in the form of his equations, which are standard in elementary population genetics texts to this day.

In concluding this 1937 paper Wright for the first time explicitly treated the surface of selective values as the surface of  $\bar{w}$ . The discussion nevertheless merely reiterates



the conclusions reached in the 1935 paper with respect to the surface of  $\bar{H}$ , which in turn derive from the non-mathematical 1932 paper:

In a large population subdivided into numerous small, partially isolated groups, the combination of directed and random divergences in gene frequencies, associated with intergroup selection, gives a trial and error mechanism under which the system of gene frequencies may pass from lower to higher peak values of  $\bar{w}$  and the species may evolve continuously even without secular changes in conditions.... The combination of partial isolation of subgroups with intergroup selection seems to provide the most favorable conditions for evolutionary advance. (1937, p. 319)

This version of the surface of selective values or adaptive landscape as the surface of  $\bar{w}$  continued to appear in all of Wright's later works (e.g., Wright, 1942, 1949, 1956, 1969, 1977), although he himself came to recognize that in any of a number of situations (e.g., frequency dependence of genotypic fitnesses, linkage) the population would not necessarily move toward peak values of  $\bar{w}$ . In fact, in his later works Wright tried to come up with some other "fitness" function that would continue to increase, even if  $\bar{w}$  was decreasing (see Wright, 1969, Ch. 5), thus struggling to maintain the metaphor for evolution that he apparently found so satisfying (Wright, 1977, Ch. 13; Wright, 1988).

What are we to make of this history? I hope it is now clear that the adaptive landscape, as conceived by Wright, is a fundamentally teleological way of thinking about evolution, based on the confusion between differences in relative fitnesses *within* populations and differences in absolute fitness (expected rate of increase) *among* populations. Although one type may have a higher relative fitness than another in a current population, this does not mean that the population as a whole would be better off in any sense if composed solely of this type.

On the other hand, if one is willing to assume constant absolute fitnesses, then a population composed solely of the type with the highest fitness would be better off than any other, in the very real sense that it would have the highest population growth rate. Nonetheless the artificiality of this assumption is so obvious that I doubt anyone would wish to support it.

None of these observations is particularly new, but it is clear that they have not been taken to heart by the majority of evolutionary biologists. If they had, then the leading American textbook of evolutionary biology would not describe the adaptive landscape metaphor as "widely used" (Futuyma, 2005, p. 403). There appears to be a strong desire among many biologists to believe that evolution, guided by natural selection, is necessarily a process of

overall improvement (Ruse, 1996). As I have tried to show above, the standard Wrightian mathematical model (or paradigm) for evolutionary change, incorporating constant "relative fitnesses," only helps to support this bias.

### Natural Selection is Not Evolution: Fisher and the Fundamental Theorem

In the second chapter of his *Genetical Theory of Natural Selection*, Fisher (1930) introduced what he called the "fundamental theorem of Natural Selection":

*The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.*

Unfortunately, the derivation of the fundamental theorem is quite difficult to follow, and the theorem has been a source of bewilderment for countless evolutionary biologists since. A large number of papers have been generated attempting to prove or disprove the theorem, or to explain what Fisher really meant (see Bennett, 1999; Edwards, 1994; Lessard, 1997).

On the surface the theorem seems to state, at the very least, that under natural selection fitness is expected to increase with time, since the genetic variance in fitness cannot be negative. Under this interpretation, the fundamental theorem seems rather similar to Wright's metaphor of the adaptive landscape, in which populations continually move toward peak values of fitness. This is in fact the interpretation that Wright himself gave it (e.g., Wright, 1935a, 1988). As it turns out, however, this interpretation is in fact a misinterpretation (one that I too was guilty of in an early version of this paper; Reiss, 1989).

The correct interpretation of Fisher's fundamental theorem was first clearly pointed out by Price (1972); more recently Ewens (1989), Edwards (1990, 1994, 2002), Frank and Slatkin (1992), Burt (1995), Lessard (1997), and Gayon (1998) have contributed some additional perspective. I will not review the mathematics here (which is largely beyond me in any case), but instead would merely like to relate Fisher's viewpoint to some of the criticisms of Wright's adaptive landscape developed above.

Before considering the fundamental theorem itself, it is necessary to briefly review its origin. In his chapter on the fundamental theorem (1930), Fisher began by introducing life tables and tables of reproduction. This allowed him to define a variable  $m$ , the "Malthusian parameter of population increase," expressing the growth rate of the population; in the ecological literature (e.g., Pianka, 1983) this is now generally called  $r$ , the "intrinsic rate of natural increase." In continuous time  $m$  is not directly related to the actual value of the population growth rate,  $\bar{R}(t)$ , as

defined in Eq. 4 above, but rather is a theoretical value that expresses the population growth rate that would occur under the stable age distribution appropriate to a population with a given system of birth and death rates. However, for populations with discrete generations,  $m$  is approximately equal to  $\ln \bar{W}$  of Wright's formulation; it is 0 for stable populations.

After defining reproductive value (not directly relevant here), Fisher went on to examine the “genetic element in variance,” distinguishing the *average excess* from the *average effect* of a gene substitution. For a pair of alleles affecting any quantitative measurement the *average excess*,  $a$ , associated with the substitution of one allele for another was defined as the difference between the mean of one of the homozygotes plus half the heterozygotes, and the mean of the alternative homozygotes plus half the heterozygotes. In contrast, he defined the *average effect*,  $\alpha$ , of the gene substitution as the average effect on the measurement, holding all other factors constant (and thus removing any correlations with other factors, as well as non-linear effects such as dominance). He then defined the genetic variance due to this factor, showing that it was equal to  $pq\alpha^2$ , where  $p$  and  $q$  were the frequencies of the alternative alleles.

In the next section, on “Natural Selection,” Fisher applied his definitions of average excess, average effect, and genetic variance to the Malthusian parameter,  $m$ , characterizing the rate of increase or decrease of individuals carrying alternative alleles at a locus. He pointed out that “ $m$  measures fitness to survive by the objective fact of representation in future generations” (p. 34). By summing over all loci, he then derived the fundamental theorem: “The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.” He cautioned that “The rigour of the demonstration requires that the terms employed be used strictly as defined...” (p. 35).

Price (1972, p. 130) noted that “The main cause of misunderstanding about the theorem is that everyone has supposed that Fisher was talking about the total change  $dM/dt$  rather than just the fraction of this due to natural selection.” Of course this is perhaps not so surprising if we recall that Fisher called the theorem the fundamental theorem of *Natural Selection*, and that the first sentence of his book stated quite clearly that “Natural Selection is not Evolution” (Fisher, 1930, p. vii).

What is perhaps surprising about Fisher's view is that “he regarded the natural selection effect on  $M$  as being limited to the additive or linear effects of changes in gene frequencies, while everything else—dominance, epistasis, population pressure, climate, and interactions with other species—he regarded as a matter of the environment” (Price, loc. cit.). Thus the fundamental theorem in effect states that the rate of increase in mean fitness (population

growth rate) that *would* occur if all genes always had constant additive effects on fitness (expected reproductive rate) is exactly equal to the (additive) genetic variance in fitness. Under this interpretation, there is no reason to think that in the circumstances actually obtaining in any real population, mean fitness (population growth rate) will necessarily increase. Price again puts this very nicely:

What Fisher's theorem tells us is that natural selection (in his restricted meaning involving only additive effects) at all times acts to increase the fitness of the species to live under the conditions that existed an instant earlier. But since the standard of ‘fitness’ changes from instant to instant, this constantly improving tendency of natural selection does not necessarily get anywhere in terms of increasing ‘fitness’ as measured by any fixed standard.... (1972, p. 131)

Although Price was “disappointed that it does not say more,” (p. 139), and felt that there was “a challenge here to find a deeper definition of this elusive concept ‘fitness’ and to give a deeper and sharper explanation of why it increases” (p. 140), the reason why Fisher's statement is in fact the only possible one should be obvious from the discussion of  $\bar{W}$  above. Since mean absolute fitness is just (expected) population growth rate, and populations can't evolve a constantly increasing growth rate, mean fitness cannot be expected to increase. Fisher himself was quite clear on this:

Against the rate of progress in fitness must be set off, if the organism is, properly speaking, highly adapted to its place in nature, deterioration due to undirected changes either in the organism or its environment. The former, typified by the pathological mutations observed by geneticists, annul their influence by calling into existence an equivalent amount of genetic variance. The latter, which are due to geological and climatological changes on the one hand, and to changes in the organic environment, including the improvement of enemies and competitors, on the other, may be in effect either greater or less than the improvement due to Natural Selection.

Any net advantage gained by an organism will be conserved in the form of an increase in population, rather than in an increase in the average Malthusian parameter, which is kept by this adjustment always near to zero. (1930, pp. 46–47)

In fact, in a 1941 paper, which well repays reading, Fisher explicitly criticised the formulation used by Wright, for many of the same reasons I have criticized it above (Fisher's critique has been quite helpful to me). In this paper Fisher insisted on the importance of the distinction



he had made between the *average excess* in fitness of an allele ( $a$ ), which is merely its expected rate of increase (rate of increase), and the *average effect* on fitness of an allele ( $\alpha$ ), which he equated with the partial linear regression of fitness (expected organismal rate of increase) on the number of copies of that allele in an organism. As noted above, it was by equating these two quantities that Wright (1935b, p. 258) was able to derive his formula for gene frequency change in the case of an intermediate optimum: “the selective disadvantage must be proportional to the momentary net effect of gene replacement on adaptive value.” The same equation lies at the base of Wright’s more general formula for gene frequency change (Wright, 1937, p. 239):

$$\Delta q_i = \frac{q_i(1 - q_i)}{2\bar{w}} \frac{\partial \bar{w}}{\partial q_i}$$

Fisher objected quite strongly to this equation on the mathematical grounds that:

...Wright’s fundamental formula is merely  $a = \alpha$ , a relationship which is certainly not true in general, or approximately true in such a variable as the survival value of different genotypes. (p. 57) The attempt to equate  $a$ , measuring the selective intensity in favor of a given gene substitution, to the average effect of that substitution on the mean fitness of the population [is] foredoomed to failure just so soon as the simplifying, but unrealistic, assumption of random mating is abandoned. (p. 58)

Fisher also objected to Wright’s mode of thinking on philosophical grounds:

In regard to selection theory, objection should be taken to Wright’s equation principally because it represents natural selection, which in reality acts upon individuals, as though it were governed by the average condition of the species or inter-breeding group. ...in Wright’s equation the whole evolutionary sequence would appear to be governed by the principle of increasing the ‘general good.’ (p. 58)

Perhaps the clearest statement of the difference that Fisher saw between his views and those of Wright is contained in a 1956 letter to Motoo Kimura, who was working on a paper discussing the fundamental theorem (published as Kimura, 1958):

In considering the original statement of what I ventured to call “the fundamental theorem of natural selection,” I had, of course, considered the relation between such a situation and that in which a potential function existed, for my mathematical education lay in the field of mathematical physics. As you realize, I

preferred to develop the theory without this assumption, which of course in another aspect is a restriction. Of course, I do not question that the selective intensities acting instantaneously may well be equivalent to those derivable from such a function, but I think it should be emphasized that both changes in time, that is in the environmental *milieu*, and in the gene ratios themselves, that is the heritable constitution of the organism, will change this virtual function in a way that cannot be specified in terms of the quantities used in formulating the fundamental theorem.

Of course I realize that Sewall Wright has often argued as though such a potential function must exist, or as though all systems of forces were conservative, and in such systems, the idea of the mean fitness of the population has, I presume, a meaning more absolute or permanent than the mean value of the Malthusian parameter actually in being. (quoted in Bennett, 1983)

An excellent discussion of the differences between Fisher and Wright on this issue can be found in a series of papers by Edwards (1992, 1994, 2000, 2002; see also Gayon, 1998). He stresses the mathematical problems associated with Wright’s adaptive landscape, particularly the interpretation of evolution as guided by a potential function,  $\bar{w}$ . He does not note, as I have emphasized here, that such a view of the evolutionary process is fundamentally teleological—because the potential derives from the difference between the current state of the population and a future improved state.

## Conclusions

The present paper is the outcome of an attempt by an outsider to the field to make sense of the way the term ‘fitness’ is defined and used by population geneticists. The definition of relative fitness,  $w$ , and mean fitness,  $\bar{w}$ , typically occurs in the first few pages of any textbook discussion of population genetics and natural selection (e.g., Griffiths et al., 2005, pp. 629–633; Hartl & Clark, 1997, pp. 212–232; Hedrick, 2000, pp. 93–94). I have argued that the textbook definition does not serve evolutionary biology well, because—through its disconnection from any real, measurable feature of a population—a vague teleology is subtly incorporated into it. I believe that models of evolution by natural selection in which mean relative fitness of populations necessarily increases are dangerous, because they suggest that evolution by natural selection is necessarily a process of improvement, while leaving it entirely nebulous what is actually being improved. If such models

were not so popular, Van Valen's (1973) "Red Queen" hypothesis would perhaps not have been so controversial.

I have proposed an alternative definition of relative fitness (standardized relative fitness = absolute fitness/population growth rate) in which genotypic fitness is allowed to vary with changes in gene frequencies. Although this alternative definition does not alter the mathematics in the slightest, in terms of predicting different outcomes for gene frequencies, it does avoid the problems with teleology that seem to beset the traditional definition, even when people are trying to be careful. It is also intuitively satisfying, in that standardized relative fitness has the precise and readily understandable meaning of the expected rate of increase in frequency. With this definition a genotype with a relative fitness  $>1$  is one that is expected to leave greater than the average number of descendants, a genotype with a relative fitness  $<1$  is expected to leave fewer than the average number of descendants.

I have also argued that Sewall Wright's model of evolution on a "surface of selective value" is closely connected to a teleology implicit in the standard equations of population genetics, and can not be understood in any other way. It is unfortunate that Wright, who was undoubtedly a great contributor to the development of evolutionary theory (Crow, 1990; Provine, 1986), should be the subject of so much recent criticism (e.g., Coyne et al., 1997, 2000; Edwards, 1994, 2000; Gavrillets, 2004; Provine, 1986). Nevertheless, for the progress of evolutionary biology it is necessary that we shed old models and prejudices in favor of an unbiased, rigorous understanding of the evolutionary process. Whether anything remains of Wright's "shifting balance theory" divorced from the metaphor of the adaptive landscape is a distinct issue, which I leave to others to decide.

In the introduction, I noted that the adaptive landscape metaphor appears to be undergoing a resurgence. For example, Arnold and coworkers have recently (Arnold, 2003; Arnold et al., 2001) argued for the usefulness of Simpson's phenotypic adaptive landscape as a conceptual bridge between micro- and macroevolution. While it is true that the variation in fitness in a population at any given time can be reasonably portrayed as such a landscape, as soon as one tries to picture the evolution of a population on such a landscape one runs into the same problems as with the gene frequency version.

Much more common today is the use of the adaptive landscape in the context of protein and nucleic acid evolution, a use dating back to Maynard Smith (1970), and more recently promoted by Kauffman and Levin (1987) and Kauffman (1993). For any given length protein or nucleic acid, one can define a "sequence space" consisting of all sequences of a given length, and assign each a fitness. This view is clearly allied to Wright's original (1932) gene

combination version of the adaptive landscape (cf. Gavrillets, 2004), though here the combinations are occurring within a single gene. How is fitness measured in such models? Kauffman (1993, p. 37) begins by defining fitness as "any well-defined property" such as "the capacity of each protein in protein space to catalyze a specific reaction under specific conditions." As with the phenotypic landscape, such a definition is certainly valid for a given population at a given time, where the specific reaction one assumes must be catalyzed is one which is already being catalyzed. To translate this into a view of the evolutionary process, however, one must assume that the need to catalyze a particular reaction is a goal toward which the evolutionary process is directed, and that improvement in this particular feature corresponds to overall improvement or "adaptive evolution," a step which he is not long in taking (1993, Ch. 4).

In the context of speciation theory, Gavrillets (2004) has recently produced an elegant synthesis of mathematical models of speciation grounded in the idea of fitness landscapes. Here he provides an excellent overview of the many versions of the adaptive landscape that have appeared, beginning with Wright (1932). Gavrillets is able to avoid most of the problems I have outlined because he insists that the adaptive landscape is only a metaphor, because he is concerned mainly to distinguish "high fitness" or viable genotypes from "low fitness" or inviable ones, and most importantly, because his preferred model of evolution on "holey landscapes" does not involve the evolution of improved mean fitness over time. Gavrillets' "holey landscapes" are essentially current genotypic fitness landscapes connected through evolutionary time to create ridges of high fitness a population can evolve along. As he points out, this is a very different vision than Wright's.

It is ironic that the teleological view that evolution by natural selection involves constantly improving adaptedness—implicit in Wright's metaphor of the adaptive landscape—has been associated by many, including Wright himself, with Fisher's "fundamental theorem of natural selection." Fisher's "fundamental theorem" of course says no such thing (Edwards, 1994). I would argue that at the level of metaphor the fundamental theorem succeeds better than the "adaptive landscape" as a model for the role of natural selection in evolution (cf. Burt, 1995). It is readily understandable at the metaphorical level (if difficult at the mathematical) that natural selection acts to increase mean absolute fitness (population growth rate), while other processes (environmental change, increased competition due to increases in population size, change in gene and genotype frequencies, mutation, etc.) act against this tendency, so that any existing population persists by virtue of a balance between all these processes.

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