Journal of Theoretical Biology 447 (2018) 190–198

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtbi

What is adaptation and how should it be measured?

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ARTICLE INFO

Article history:
Received 17 May 2017
Revised 27 February 2018
Accepted 4 March 2018
Available online 6 March 2018

Keywords:
Evolution
Natural selection
Biological information
Biological complexity
Population genetics

ABSTRACT

Adaptation is a defining property of living systems. It occurs when organisms become better suited to their environment. The phenomena that people find most fascinating about biological systems are, in general, the result of adaptive processes. Examples include the mammalian central nervous system, the flight of birds and insects, photosynthesis, and the human hand. However, despite the centrality of adaptation for biology, there is no generally agreed *quantitative* way to describe the degree to which an organism is adapted. Here, we address this situation by proposing a quantitative measure of adaptation. We also present results of computer simulations which demonstrate that some changes in parameter values cause mean adaptedness and mean relative fitness to change in opposite directions. This indicates that adaptedness and relative fitness are distinct concepts. We suggest that the measure of adaptedness proposed in this work may help to resolve questions about 'units of selection' and 'major transitions in evolution'.

1. Introduction

Adaptation is a key concept for biological evolution (Brandon, 2014; Reeve and Sherman, 1993; Williams, 1966). Indeed, the observation of adaptation was a central motivation for Darwin's development of the theory of evolution by natural selection (Darwin, 1859). However, at present, scientific investigation of adaptation is impeded because evolutionary biologists have no satisfactory *quantitative way* to describe the degree to which an organism is adapted to its environment.

A satisfactory quantitative measure of adaptation would allow for investigation into how various environmental and genetic variables affect the development and maintenance of adaptation (Williams, 1966). Such a measure of adaptation can also be expected to advance research on 'units of selection', and on closely-related issues associated with 'major transitions in evolution' (Keller, 1999; Lewontin, 1970; Maynard Smith and Szathmáry, 1995; Williams, 1966). To a substantial extent, these two topics relate to the degree to which biological adaptation occurs at the level of groups of organisms. Thus, a tool that allows for the quantitative measurement of adaptedness may well prove to be indispensable for the solution of some of the deepest and most vexing problems in contemporary evolutionary biology.

Here, we propose a quantitative measure of adaptation, and we test it using computer simulations of biological populations. Our adaptedness measure is assessed on individual organisms. The adaptedness of an entire population can be assessed by simply taking the mean of the proposed adaptedness measure over the population.

There have been some previous attempts to quantify adaptedness (Brandon, 2014; Reeve and Sherman, 1993). The most pertinent idea appears to be that of R. Brandon, who said that if we compare two organismal types, whether genotypes or phenotypes, then the organismal type associated with higher biological fitness (i.e., with higher reproductive success) is also the better adapted (Brandon, 2014). If we have a set of many organismal types, Brandon's proposal allows us to arrange them in order of adaptedness. Of course, this ordering is not an intrinsic quality of the organismal types. Rather, it is a determined, in part, by the nature of the environment within which the population lives. This is because, in Brandon's conception, adaptation is a function of the fitness of the various possible organismal types, and fitness depends on environmental conditions.

Brandon's proposal seems to accord with the natural-language meaning of adaptedness, and the work reported here is based upon it. However, Brandon's proposal does not provide a satisfactory quantitative measure, since it does not convey the degree to which one type is more (or less) adapted than another. That is to say, it is merely an 'ordinal measure' of adaptedness (Stevens, 1946).

Perhaps the reason that we have no satisfactory quantitative measure of adaptation is that such a measure may appear to be redundant. At first glance, it seems that the concept of biological fitness already provides such a measure. After all, fitness is a continuous variable, and, as Brandon suggests, if one type is fitter

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https://doi.org/10.1016/j.jtbi.2018.03.003
0022-5193/

than another, then it is also sensible to say that it is better adapted (Brandon, 2014; Futuyma, 2013).

However, some reflection reveals that fitness can easily fail as a measure of adaptation. To see why, let us begin by considering the simple case of *absolute fitness* for a population of asexual organisms with discrete generations and with no 'class structure' (Grafen, 2006a, 2015). Here, the absolute fitness of a newborn individual is the expected number of offspring that the individual will contribute to the next generation. Thus, absolute fitness is equal to expected reproductive success, and it takes into account both *viability* and *fertility*. That is to say, absolute fitness is affected both by the probability that a newborn individual will survive to reproductive age, and by the expected number of offspring that the newborn individual will have, if it survives.

Let us assume, for the asexual organism under consideration, that the population size stays approximately constant from generation to generation. Under this assumption, in a population like the one just described, the mean value of absolute fitness must be approximately equal to one. This is true regardless of whether all population members have the best-possible organismal type, or if their organismal types are far from optimal. Accordingly, the mean of absolute fitness for the population is *independent* of the appropriateness of the organismal types present in the population for the current environmental conditions. As such, absolute fitness cannot be a good measure of adaptedness (Barton, 2017).

One might think that the problems associated with using absolute fitness to measure adaptedness could be eliminated by using *relative fitness* instead. The relative fitness of a newborn individual is equal to the individual's absolute fitness divided by the absolute fitness of a newborn with some reference organismal type. Here, we will take the reference type to be an organismal type with the maximum-possible value of absolute fitness. Unfortunately, relative fitness also fails as a measure of adaptedness. The reason for this is more subtle than in the case of absolute fitness.

To understand the problems with using relative fitness as an adaptedness measure, it is helpful to consider the case of purifying selection that constrains a phenotypic trait to be close to a particular optimum state. We might, for instance, imagine an organism that is occasionally afflicted with a parasite. Assume that this organism can produce a particular protein that inhibits the parasite and thus enhances relative fitness. Assume further that there is an optimal amino-acid sequence for this protein, and each mutation that causes a difference from this optimal sequence decreases the effectiveness of the protective protein, and thus leads to a decrease in relative fitness.

In a simple mathematical model of this sort of situation (presented below) we consider how the strength of selection affects the mean value of relative fitness, when measured after evolution has proceeded for thousands of generations. The strength of selection may depend, for example, on the density of the parasite. We show that the mean of relative fitness *increases* as the strength of selection decreases. However, when the strength of selection is very low, a typical individual has an extensively mutated protective protein, with a sequence that is very different from the optimal sequence. That is, when selection is weak, the typical individual is *poorly adapted* to the environment. It follows that decreasing the strength of selection has the simultaneous effect of increasing mean relative fitness, but decreasing the mean value of adaptedness. The opposite directions of change of mean relative fitness and mean adaptedness explicitly demonstrate that relative fitness provides an inadequate quantitative measure of adaptation. Below, we illustrate this phenomenon using computer simulations. We also present another (quite different) case in which adaptedness and relative fitness respond in opposite directions to a change of parameter values.

2. A quantitative measure of adaptedness

To begin our development of a quantitative measure of adaptation, let us consider a species in which we can identify Ω different types of individual. A particular organismal type may be defined by any aspect of an individual's genotype or phenotype, or by a description that includes aspects of both genotype and phenotype. We number these different organismal types $1, 2, 3, \ldots, \Omega$, and will refer to the collection of all Ω types as the *comparison set*.

Let w_i represent the relative fitness of newborn individuals that have the ith organismal type. That is, w_i represents the expected reproductive success of type i newborns, divided by the expected reproductive success of newborn individuals that have an organismal type that confers the maximum-possible level of expected reproductive success (maximising over all members of the comparison set). Thus, $0 \leq w_i \leq 1$.

In light of the foregoing discussion, we propose the following two requirements for a quantitative measure of adaptedness:

(1) A quantitative measure of adaptedness should be an increasing function of relative fitness. That is, if, in a given environment, $w_i > w_j$, then type i is better adapted than type j in that environment.
(2) The value of adaptedness, for a given organismal type, should reflect how special that type is for a particular environment. That is, it should indicate the extent to which the organismal type is unique with respect to how high its relative fitness is in the environment.

We now propose a particular measure of adaptedness which is both reasonably simple, and which satisfies both of these requirements.

Let α_i denote the adaptedness of type i. Let Q_i represent the number of organismal types in the comparison set that have a level of relative fitness that *equals or exceeds* the relative fitness of organismal-type i in a given environment. Our measure of adaptedness is

$$\alpha_i = \log_2\left(\frac{\Omega}{Q_i}\right). \tag{1}$$

where $\log_2$ denotes a logarithm to base 2. We will refer to α_i simply as the *adaptedness* of type i. It should be noted that $1 \leq Q_i \leq \Omega$, and hence $0 \leq \alpha_i \leq \log_2(\Omega)$.

The adaptedness measure specified by Eq. (1) is a special case of "functional information", as defined by Hazen et al. (2007) and Szostak (2003). Szostak developed the idea of functional information as a way to "define and quantify the information content of biopolymer sequences" (Szostak, 2003). Similar motivations also led C. Adami and his colleagues to develop a quantity that is very similar (or identical) to Eq. (1) (see their Eq. (12)) (Adami et al., 2000). Neither Szostak nor Adami et al. suggested using a quantity of the form given by Eq. (1) as a measure of adaptedness. The connection between adaptedness and information is discussed below.

In the interests of clarity and analytic convenience, we restrict ourselves, in this work, to comparison sets that contain a finite number of discrete organismal states (e.g., genotypes). However, it seems certain that, by an appropriate generalisation, the analysis presented here can be extended to cases in which the number of organismal types is infinite, as it is the case when organismal type is defined by a continuously distributed phenotype such as height or weight.

It is clear that the definition of the adaptedness of type i, namely α_i that is given in Eq. (1), satisfies requirement (1), above. That is, if one organismal type is better adapted than another (as measured by α_i) then it will also have a higher relative fitness. A little consideration reveals that the definition of α_i also satisfies requirement (2). In particular, if the fraction $\frac{\Omega}{Q_i}$ is very large, then

this means that, of all types within the comparison set, type i is very unusual in that it has a level of relative fitness that is higher than almost any other type. In such a case, type i is very special (indeed, it is almost unique) in being so well-suited to the environment. Thus, appropriately for this case, α_i will be relatively large. Alternatively, if more than 50% of types in the comparison set are at least as fit as type i, then α_i will be relatively small (i.e., between zero and one). The adaptedness, α_i, equals zero if all types in the comparison set are at least as fit as type i.

It may be worth considering the adaptedness of a randomly selected organismal type. Let us assume that the relative fitness of each organismal type is drawn from a continuous probability distribution, and let us consider the limit as the number of organismal types (Ω) becomes very large (that is, $\Omega \to \infty$). In this case, the expected value of adaptedness is shown in Appendix A to equal the relatively small value $1/\ln(2) \approx 1.443$. The standard deviation in adaptedness among such randomly-selected organismal types is also shown to be given by $1/\ln(2)$.

To put this result in context, we note that a randomly selected organismal type will have a value of adaptedness, α_i, of zero with probability of $1/\Omega$, while a randomly selected organismal type is likely to have a small positive value of the adaptedness. That is to say, even if selection has had no effect on the distribution of organismal types, a typical organismal type will have some level of 'pre-adaptation' purely by chance. Only the organismal types with the very lowest relative fitness have no pre-adaptation, and thus these types have an adaptedness of zero.

Because the measure of adaptedness proposed in this work satisfies requirement (2), it also is in line with the views of those biologists (including Darwin) who identify adaptation with the way that so many biological structures and behaviours seem "designed" to enhance reproductive success (Darwin, 1859; Gardner, 2009; Grafen, 2007). The impression that a biological structure or behaviour is similar to designed objects comes from observations that the structure or behaviour is relatively unique in its tendency to enhance reproductive success. That is, these structures and behaviours seem to be the result of some sort of (possibly imperfect) optimisation process (Gardner, 2009; Grafen, 2007). The proposed measure of adaptedness quantifies the degree to which an organismal type is unique in its ability to enhance reproductive success, and this provides a link to the ideas of biologists who have associated adaptation with apparent design.

2.1. Dependence of adaptedness upon the comparison set

In order to use Eq. (1) to quantify the adaptedness of a particular type, we must first identify the entire set of Ω organismal types that will be used for a comparison. The choice of this comparison set is somewhat arbitrary.

In some cases, one may wish to choose a natural comparison set. For example, if organismal type is defined by genetic sequence, then one may wish to choose a comparison set containing all of the genetic sequences that can be constructed for a given total sequence length. Another possibility is to pick a well-defined genetic region, such as a gene or a crucial sequence within a gene, and use a comparison set that contains all possible sequences that could occur in this genetic region. All members of this comparison set could have the same genetic sequence outside of the focal region, with this sequence being chosen to be typical in a particular natural population. Using such a comparison set, one could investigate the effect on adaptation of variation in a relatively constrained region of the genome.

Of course, natural comparison sets may not exist for every analysis that one might wish to carry out. For example, one may wish to compare a particular genetic sequence found in a natural population with all alternative sequences that can be created with fewer than a certain number of nucleotide changes. The number of such changes may be determined by practical considerations, and hence this number may have no natural biological significance. This is unfortunate, as the form of Eq. (1) only allows us to measure adaptedness in the context of a particular comparison set. However, this arbitrariness is less consequential than it might seem at first sight. This is because, in a *comparison* of the adaptedness of two types, the same answer is obtained for many different comparison sets. In particular, consider two types, i and k, with adaptedness values α_i and α_k, respectively. Let D represent the difference between the two adaptedness values, given a particular comparison set that contains Ω different types (thus $D = \alpha_i - \alpha_k$). Let us now create a new, larger comparison set that contains all Ω organismal types of the original comparison set, *plus* an additional set of types that all have a *lower* relative fitness than that of both type i and type k. Let $\breve{\alpha}_i$ and $\breve{\alpha}_k$ represent the adaptedness values of type i and type k for this new, larger comparison set. In Appendix B we show that the difference in adaptedness between the two types is unchanged by this alteration in the size of the comparison set (i.e., $D = \alpha_i - \alpha_k = \breve{\alpha}_i - \breve{\alpha}_k$).

2.2. Why use a logarithmic measure to quantify adaptation?

In terms of the requirements for an adaptedness measure specified above, any monotonically-increasing function of the ratio $\frac{\Omega}{Q_i}$ could serve as a measure of adaptedness. However, there are three reasons for using a logarithm in this context. First, comparison sets can be very large. For example, the bacterium *Candidatus Carsonella ruddii* has one of the very smallest bacterial genomes, with only 159,662 base pairs (Nakabachi et al., 2006). If one constructed a comparison set with every possible DNA genome of this length, then the comparison set would have approximately $10^{96,126}$ members. Thus, in this case, if we simply used the ratio $\frac{\Omega}{Q_i}$ as adaptedness measure, all of the fittest genotypes would have huge numbers as their adaptedness scores. Numbers of this magnitude are unwieldy, and not very amenable to informal thinking. It is much more convenient (and comprehensible) to refer to numbers of this size using exponents, and this is exactly what occurs when one uses logarithms. Thus, for example, if there is a unique genome of *C. ruddii* that is fittest in a particular environment, then, using our logarithmic measure, its adaptedness value would be 319,324. This is much more comprehensible than $10^{96,126}$, which would be the adaptedness value if we were to simply use $\frac{\Omega}{Q_i}$ as our adaptedness measure.

A second reason for using a logarithmic function for the adaptedness measure is the way that adaptedness changes with Q_i. For example, consider what would happen if, instead of using a logarithmic function, we simply use the ratio $\frac{\Omega}{Q_i}$ as our adaptedness measure. Let us again take the example of a genome of the length we have in *C. ruddii* (i.e., 159,662 nucleotides), and let us calculate the ratio of adaptedness values that has as its numerator the adaptedness value of an organism that has a genome that is better than all but 1024 other sequences, with the denominator given by the adaptedness value for an organism with a genome that is uniquely the best that can be constructed with 159,662 nucleotides. (It might be possible to construct the less-adapted genome by substituting sub-optimal nucleotides into the optimal genome at 5 loci.) Using this non-logarithmic form of an adaptedness measure, the ratio of adaptedness values is equal to $\frac{1}{1024}$ (i.e., the ratio is approximately equal to 0.001). This seems like a very small value, given that it is supposed to represent the relative adaptedness of two organisms that both have genomes that are more fit that all but an almost-infinitesimal fraction of the set of possible genomes. On the other hand, if we use our logarithmic measure (i.e., α_i, as given by Eq. (1)) then the ratio of the two

adaptedness measures is approximately 0.99997, which seems like a much more sensible result.

The final reason for using a logarithmic measure (to base 2) is that it allows for comparison of our adaptedness measure with various measures of "biological information" (Barton, 2017; Frank, 2012; Watkins, 2008). Using a logarithmic measure also facilitates comparison with the information-theoretic concept of "biological complexity" (Adami and Cerf, 2000; Adami et al., 2000). A detailed analysis of these subtle concepts is beyond the scope of the current work. However, an inkling of the importance of the possible connection between adaptedness and information can be obtained by considering the amount of information that would be required to specify a particular region of "genotypic space" that contains optimal genotypes.

Say that we collect all possible genotypes of a particular length into groups, such that for each group, the maximum *Hamming distance* between group members is less than some integer, which we will call R. (The Hamming distance between two genotypes is just the number of nucleotide changes that one must make to transform one of the genotypes into the other.) Assume that every genotype is a member of only one of these groups, and that there are a total of M groups all together, with T genotypes in each group (thus, there are a total of MT genotypes). Now say that there is a unique optimal genotype that has the maximum value of relative fitness, and that the relative fitness of all other genotypes is a decreasing function of their Hamming distance from this optimal genotype. In this case, according to Eq. (1), the adaptedness of each of the members of the group of genotypes that contains the optimum must be equal to (or greater than) $\log_2(\frac{MT}{T}) = \log_2(M)$. Furthermore, if we number the groups of genotypes as $1, 2, \ldots, M$, and then ask how many digits are required to guarantee that we can specify the number associated with the group containing the optimal genotype, the answer is approximately equal to $0.301\ \log_2(M)$ digits. (If we number the genotypes in base 2, then the number of digits required will be approximately equal to $\log_2(M)$.) The number of digits required may be seen as a measure of the amount of information necessary to specify the optimum-containing group (Cover and Thomas, 1991). Thus, there is a correspondence between the adaptedness values of the fittest-possible genotypes, and the amount of information required to specify a group containing these individuals. This example suggests that there may be a close relationship between biological information and adaptedness, if we measure adaptedness on a logarithmic scale.

3. Model

To see the proposed measure of adaptation in use, let us consider a specific model of genetic evolution. Assume a population that is haploid, with L genetic loci, and 4 possible alleles per locus. There are, therefore, 4^L possible genotypes, which we label $1, 2, 3, \ldots, 4^L$. Generations are discrete, so members of the parental generation may be taken to die after all offspring of their generation have been born. After birth, viability selection occurs, and the probability of an individual surviving selection is assumed to depend only on the individual's genotype. For individuals with genotype i, this survival probability is denoted by V_i. There is then a "thinning process" during which additional randomly chosen individuals die, leaving a population that contains exactly N individuals. These N individuals constitute the potential parents for the next generation, and are therefore considered to be adults.

Except where noted otherwise, the population reproduces sexually. To produce an offspring, two adults are chosen at random as parents, and the offspring's genome is produced via sexual reproduction with free recombination between loci (the allele at each locus of an offspring's genome has an equal chance of coming from either parent). Mutations occur during reproduction at a rate of μ per allele copied, and each mutation results in a change from the parental allele to one of the other three alleles, with equal probability. Sufficient offspring are assumed to be produced so that, after viability selection, the number of individuals remaining in the population is always in excess of N.

Under the assumptions of this model, all adults have the same expected fecundity, and thus the only factor that can affect relative fitness is the differences in viability between the various genotypes. Therefore, if we use w_i to denote the relative fitness of genotype i, then we have:

$$w_i = \frac{V_i}{V_{max}}, \tag{2}$$

where V_{max} is the maximum of all of all of the V_i values.

Let us now consider a particular fitness scheme for this model. We shall adopt a well-known single-peak 'landscape' with an optimal genotype, where each genetic difference from the optimal genotype decreases viability (and thus relative fitness) by a factor of $(1-s)$, where $0 \leq s \leq 1$. Thus, if there are k loci at which genotype i differs from the optimal genotype, then the viability of this genotype is given by $V_i = V_{max}\ (1-s)^k$. As a result, from Eq. (2), we also have $w_i = (1-s)^k$.

It can be shown mathematically that an evolving population of the sort just described constitutes an ergodic process. That is to say, after a sufficiently long period of time has passed, the state of the population is guaranteed to become independent of the initial state of the population. Here, our main interest is in how the population behaves over the long term. Therefore, we initialised each population with N mutation-free adults. We then waited 7500 generations before beginning to record the data that is summarised below. In order to ascertain whether 7500 generations are sufficient to achieve independence from initial conditions, we also ran trials with a variety of other initial populations. In doing this, we focussed on the cases where the establishment of independence from initial conditions takes the longest. Comparisons of results obtained with different initial conditions suggest strongly that, for all cases studied here, 7500 generations is sufficient to establish virtual independence of the state of a population from the initial state of the population.

Using this single-peaked fitness model, let us now consider the effects of changing the strength of selection, as measured by the value of s. For convenience, we use the complete collection of all 4^L possible genotypes as our comparison set. Thus, $\Omega = 4^L$. Furthermore, except where noted otherwise, we use a population size of $N = 10{,}000$.

3.1. Computer-simulation results

Fig. 1 presents the results of this model when the number of loci is $L = 500$, for various values of s (where s represents the strength of selection). Note that, as s decreases towards zero, the mean relative fitness increases monotonically. This result differs from some classical results, and we explain this in the discussion. As selection becomes weaker (i.e., as s becomes smaller) there is also a monotonic increase in the average number of genetic differences (the Hamming distance) between genomes in the population and the optimal genome (see Table 1). Thus, with weakening selection, the genome of a typical individual becomes more genetically distant from the optimal genotype, and hence progressively less reliable as an indicator of the position of the selective optimum. That is, the population becomes less adapted. This is reflected in the way that the mean value of α_i during a particular generation (denoted by $\bar{\alpha}$) decreases as the strength of selection, s, decreases.

Under the model's assumptions, viability is the only way that genotype can affect relative fitness. Thus, the fact that changes

Table 1
Data from the computer simulations. The unbracketed figures are arithmetic means, representing an average over the last 92,500 generations of a simulation run, of the indicated quantity. The figures in round brackets give standard deviations that indicate how much the relevant statistic varies over the last 92,500 generations of a simulation run. "Mean num. mutations" is the mean number of deleterious mutations per individual. Except where noted otherwise, the parameter values used in the simulations were: $N = 10{,}000$, $L = 500$, and $\mu = 0.002$. Data were collected each generation immediately after birth. In all the simulations reported in this study, the expected number of offspring per adult was 15.

	$s = 0.001$	$s = 0.01$	$s = 0.1$	$s = 1.0$	$s = 0.01$ $L = 50$ $\mu = 0.02$	$s = 0.01$ $L = 50$	Asexual ($s = 0.01$)
Mean viability	0.716 (0.00114)	0.394 (0.00270)	0.370 (0.00265)	0.368 (0.00125)	0.715 (0.00108)	0.911 (0.00189)	0.0979 (0.00471)
Mean num. mutations	334.489 (1.588)	92.941 (0.683)	9.934 (0.0712)	0.999 (0.00257)	33.393 (0.150)	9.281 (0.207)	231.537 (4.746)
Mean adaptedness ($\bar{\alpha}$)	15.719 (0.951)	511.356 (2.537)	917.571 (0.509)	989.898 (0.0251)	3.613 (0.116)	54.065 (0.760)	139.663 (8.606)

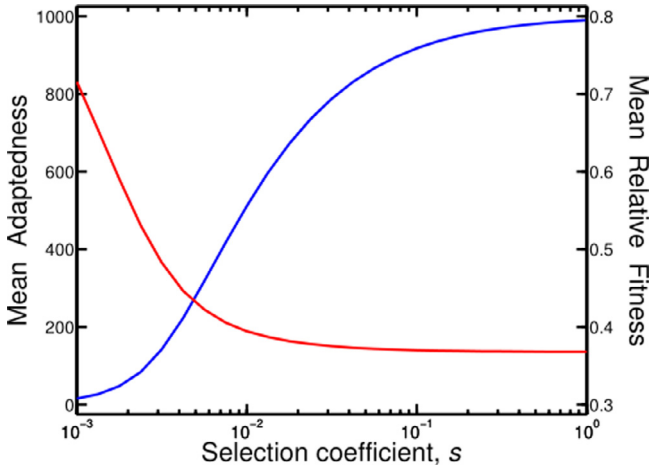

Fig. 1. Data from the computer simulations. We plot mean adaptedness and mean relative fitness as a function of the selection coefficient, s, which is a measure of the strength of selection. The right-hand vertical axis and the red curve give the data for mean relative fitness. The left-hand vertical axis and the blue curve give the data for mean adaptedness. We represent mean relative fitness and mean adaptedness during a given generation with the symbols $\bar{w}$ and $\bar{\alpha}$, respectively. The data shown by the red line gives the arithmetic mean of $\bar{w}$, averaging over the last 92,500 generations of a computer-simulation run. Similarly, the data shown by the blue line shows the arithmetic mean of $\bar{\alpha}$, averaging over the last 92,500 generations of a computer-simulation run. Parameter values used in these simulations are: $N = 10{,}000$, $L = 500$, $\mu = 0.002$, and $V_{max} = 1$. All simulations were run for 100,000 generations. The populations were censused each generation immediately after the birth of the offspring. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

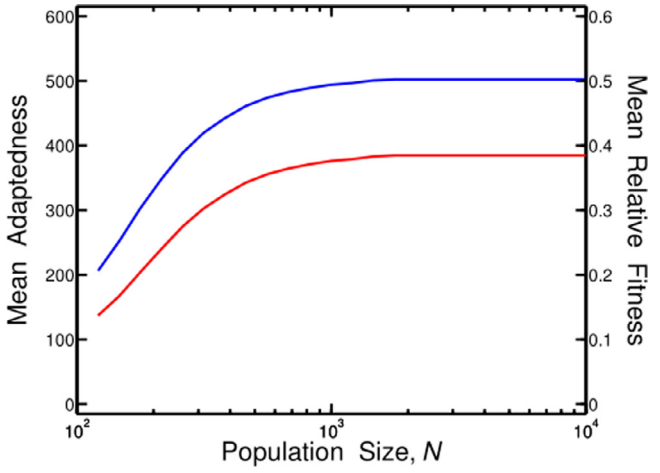

Fig. 2. Data from the computer simulations. We plot mean adaptedness and mean relative fitness as a function of the population size, N. The right-hand vertical axis and the red curve give the data for mean relative fitness. The left-hand vertical axis and the blue curve give the data for mean adaptedness. We represent mean relative fitness and mean adaptedness during a given generation with the symbols $\bar{w}$ and $\bar{\alpha}$, respectively. The data shown by the red line gives the arithmetic mean of $\bar{w}$, averaging over the last 92,500 generations of a computer-simulation run. Similarly, the data shown by the blue line shows the arithmetic mean of $\bar{\alpha}$, averaging over the last 92,500 generations of a computer-simulation run. Parameter values used in these simulations are: $s = 0.01$, $L = 500$, $\mu = 0.002$, and $V_{max} = 1$. All simulations were run for 100,000 generations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in the value of s have opposite effects on mean relative fitness and mean adaptedness makes it very clear that relative fitness is not generally suitable as a measure of adaptedness (as indicated above). A similar effect can be seen if we consider the impact of decreasing the number of loci from $L = 500$ to $L = 50$. As shown in Table 1, this leads to an increase in mean relative fitness, and a decrease in mean adaptedness, $\bar{\alpha}$. Furthermore, this is so regardless of whether we leave μ (the per-locus mutation rate) unaltered as we change the number of loci, or if we increase μ by a factor of 10, and thus keep unchanged the average number of new mutations per genome. For example, when $s = 0.01$ (with $N = 10{,}000$ and $\mu = 0.002$), decreasing L from 500 to 50 *increases* the mean relative fitness from 0.394 to 0.911, but this decrease in L also results in the mean adaptedness *decreasing* from 511.356 to 54.065.

The results are very different if we consider the effect of changing the population size. Fig. 2 shows that, as population size increases, so do both mean relative fitness and mean adaptedness. Thus, there seems to be no general rule about whether these two statistics change in the same direction as a consequence of the change in a parameter, or in opposite directions. Once again, this demonstrates that, in general, adaptedness and relative fitness are different phenomena. Mean relative fitness measures the average reproductive success of population members, in comparison with individuals that have the best-possible organismal type. Mean adaptedness, on the other hand, essentially measures the extent to which population members tend to have one of the fittest-possible organismal types. These two measures are obviously related, but they are not the same thing.

Let us now consider the effects of asexual reproduction on relative fitness, and on adaptation. The model described above incorporates sex and free recombination. To model asexuality, we use the same model, except that each offspring has only one parent. Apart from new mutations, the genomes of offspring are identical to the genomes of their parents. Asexuality enhances the correlation in relative fitness between parent and offspring. In a finite population, this generally depresses relative fitness (in comparison to sexual populations) (Crow and Kimura, 1970; Hill and Robertson, 1966; Peck et al., 1997). As can be seen from Table 1, asexuality can also decrease mean adaptedness ($\bar{\alpha}$). Thus, we have a second example of a change in parameter values affecting both mean relative fitness and mean adaptedness in the same direction. Many

other aspects of life history, genetics, and demography can be explored in a similar fashion.

4. Discussion

In this study, we have proposed a quantitative method for measuring adaptedness. We have attempted to demonstrate that the proposed measure is in line with what biologists typically mean when they talk about adaptation (Brandon, 2014; Gardner, 2009; Reeve and Sherman, 1993; Williams, 1966). Furthermore, we have shown that adaptedness is not just relative fitness in another guise, but an independent entity. Thus, for example, if we compare two populations and find that average relative fitness is higher in the first population (compared with the second) then this does not imply that the first population will also have a higher average level of adaptedness. Indeed, just the opposite may be the case (as shown in the computer-simulation results). With these considerations in mind, it is plausible that an intuitively acceptable quantification of adaptedness will facilitate the empirical study of adaptation. Given the centrality of adaptation for evolutionary biology, this outcome, if realised, would be a substantial advance.

4.1. Considerations regarding the relationship between the strength of selection and mean relative fitness

In our computer simulations, we found that the long-term value of mean relative fitness increased monotonically as the strength of selection (s) was decreased. This is very different from some classic results, in which the equilibrium mean relative fitness is independent of the strength of selection (Crow and Kimura, 1970). The main reason for this difference is that, in our model, each allele was equally likely to mutate into each of the alternative alleles. Had we assumed that: (i) only deleterious mutations are possible, and (ii) the population size is infinite, then the equilibrium mean relative fitness would have been independent of the strength of selection, as in the classic models (Crow and Kimura, 1970). However, this situation is unrealistic, as no natural population is of infinite size. In a finite population with only deleterious mutations, the population will inevitably degenerate, as deleterious mutations become fixed (Lynch et al., 1993, 1995). As a consequence the mean relative fitness will reduce over time and will eventually reach its lowest-possible value. The finite populations of our simulations were saved from this fate because deleterious mutations could (occasionally) mutate into optimal alleles.

4.2. Considerations regarding the measurement of adaptedness

One potential problem with using the proposed measure of adaptedness in empirical studies is the very large size of many comparison sets that might be of interest. Even for a small genome, the number of possible configurations can be immense. If the comparison-set size is much larger than the population size, then many organismal types may never arise, even if one waits for a long time.

However, the difficulty with large comparison sets, while real, may not be as challenging as it first appears. After all, to evaluate the adaptedness of a particular organismal type (the *focal type*) one need not ascertain the exact relative fitness of all other types. Rather, one need only decide, for each type, whether it is more or less fit than the focal type. Often, it should be possible to do this via a process of interpolation, or on the basis of knowledge of the biology of the system. Furthermore, if some of the organismal types that are fitter than the focal type are mistakenly taken to be less fit than the focal type (and vice versa), this will not greatly affect the value of adaptedness (α_i) that is calculated, providing that the error rates are sufficiently small.

Another approach is to simply focus on relatively small comparison sets. For example, if very few population members have more than, say, 10 differences from some locally optimal genotype, then one might exclude all genotypes with more than 10 differences from the optimum from the comparison set. Such an approach can allow one to describe quantitatively how close various sorts of organisms are to local optima. However, a problem with relatively small comparison sets is that a species that is capable of finding the best of several local optima might appear to be no better adapted, with such a comparison set, than a species that always evolves towards the nearest local optimum, even if more distant optima are associated with much higher levels of relative fitness. In order to notice the superior adaptive powers associated with species that can find the best of several local optima, one would need a comparison set sufficiently large to encompass multiple local optima.

An additional consideration regarding the measurement of adaptation in the present study is that we have assumed certain symmetries. In particular, in our computer simulations, we assumed that all alleles are equivalent in that all possible allelic mutations occur at the same rate at every locus. While this sort of simplifying assumption is common in models of population genetics, it should be recognised that modification of the proposed adaptedness measure may be appropriate in less symmetric situations.

4.3. Considerations regarding the measurement of fitness

In the computer-simulation studies described above, the hypothetical populations involved no class structure, no age structure, and no social interactions that could affect reproductive success. As such, it was appropriate to measure fitness in terms of the expected number of offspring that a newborn individual will have in the next generation. However, in more complex models, such as those involving multiple classes of individuals or overlapping generations, other fitness measures may be more appropriate (Crewe et al., 2018; Fisher, 1930; Grafen, 2006a, 2015; Lessard and Soares, 2016).

In some cases there are multiple reasonable choices that one might make in selecting a fitness measure. These choices are important, as they affect the fitness values that one will calculate, and as a consequence, they also affect adaptedness values. For example, in kin-selection models, one may choose to use either some measure of 'inclusive fitness', or 'neighbour-modulated fitness' (Hamilton, 1964a; Taylor et al., 2007). Roughly speaking, inclusive fitness measures the expected success of an individual in generating living individuals in future generations. These individuals may be generated via direct reproduction, by assisting others to reproduce, or by interceding to prevent the death of others. The calculation of inclusive fitness involves 'weighting' each of the individuals generated by the degree of relatedness between that individual, and the individual that facilitated their birth or that acted to preserve their life. Neighbour-modulated fitness, on the other hand, relates to an individual's personal reproductive success (i.e., the number of offspring that they produce) as determined, in part, by social interactions.

It is generally held that, when properly handled, inclusive fitness and neighbour-modulated fitness will typically produce similar (or identical) predictions regarding the long-term outcome of evolution (Hamilton, 1964a; Taylor et al., 2007). However, these two approaches constitute very different perspectives on evolution. To see this, consider the case of sterile workers. In some bees, ants, and wasps, sterile workers comprise the vast majority of population members (Hamilton, 1964b; Wilson, 1975). For all of these individuals, the neighbour-modulated fitness is zero (because they are sterile), and thus, if we use the neighbour-modulated measure

of fitness, their adaptedness is also zero. This observation suggests that, when social interactions are important, it may be worthwhile to use inclusive fitness as the fitness measure used to determine adaptedness values. However, there is still considerable controversy over the details of how inclusive fitness should be measured, and researchers will have to make their choices about this matter depending both upon the nature of the system with which they are working, and upon the scientific questions that they are trying to answer (Birch, 2017; Gardner et al., 2011; Grafen, 2006b; van Veelen et al., 2012, 2017).

4.4. Considerations regarding the units of selection

In addition to facilitating the study of adaptation, the measure of adaptedness proposed here may also help to bring quantitative rigour to the study of the 'units of selection', and the related issue of the 'major transitions in evolution' (Brandon, 1999; Keller, 1999; Maynard Smith and Szathmáry, 1995; Wilson and Sober, 1989). These transitions were identified by J. Maynard Smith and E. Szathmáry, and one type of transition is when multiple organisms combine together to form an integrated group that can be regarded as a new, higher-level organism (Keller, 1999; Maynard Smith and Szathmáry, 1995). The constituent individuals that make up this 'super-organism' may be derived from a single species, or from multiple species.

When organisms unite to form a new integrated superorganism, we have, in essence, had a change such that natural selection is now effective at a higher level of organisation than was the case before the unification. Thus, most of the major transitions in evolution described by Maynard Smith and Szathmáry are special cases of evolutionary change that leads to an alteration in the importance of various units of selection (Keller, 1999; Lewontin, 1970; Maynard Smith and Szathmáry, 1995).

To see how our measure of adaptedness might facilitate quantitative studies of the units of selection, let us examine a simple example. Consider an organism which has discrete generations, and for which there are Ω possible organismal types. Assume that this organism lives in groups, each of which contains Λ individuals. Let us say that we can use some rule to measure the group-level relative fitness for each group in the population. For example, the group-level relative fitness for a particular group might be proportional to the number of individuals in the next generation that are descended from members of that group. We could then generate a set of organismal types for groups. For example, the organismal type of a group might be determined by the combination of organismal types of the group members. The number of possible combinations of this sort is equal to $\frac{(\Omega+\Lambda-1)!}{\Lambda!(\Omega-1)!}$ (Benjamin and Quinn, 2003). Thus, if $\tilde{\Omega}$ is the number of possible organismal types for the group, then $\tilde{\Omega} = \frac{(\Omega+\Lambda-1)!}{\Lambda!(\Omega-1)!}$.

Clearly, $\tilde{\Omega}$ can be vastly greater than Ω. Thus, for example, if $\Omega = 10$ and if there are two individuals per group, then $\tilde{\Omega} = 55$. For 10 individuals per group, $\tilde{\Omega} = 92{,}378$. And if there are 100 individuals per group, $\tilde{\Omega} = 4{,}263{,}421{,}511{,}271$.

The maximum possible value of adaptedness is equal to the logarithm of the number of possible organismal types. Thus, the potential for adaptation is typically much larger for a group of substantial size than it is for any of the individual group members. For example, if, again, $\Omega = 10$, then the maximum possible value of adaptedness for individuals is 3.322. However, for a group of size two, the maximum level of adaptedness for the group 5.781, which is nearly double the maximum-possible adaptedness for individuals. For groups of size 10 and 100, the maximum-possible adaptedness for the group increases to 16.495 and 41.955, respectively. (Note that all of these maxima are calculated after assuming that each organismal type has a unique level of relative fitness.)

It is clear that, in some cases, the potential for higher levels of adaptation are realised when groups of organisms become more-or-less aligned in their evolutionary interests. Prime examples of this include the 'major transitions' mentioned above. A particularly clear case is the rise of the eukaryotes, which involved the formation of groups of two different types of organisms, one of which is the ancestor of the mitochondria in modern eukaryotes, and the other of which is the ancestor of nuclear genomes (Maynard Smith and Szathmáry, 1995; Zimorski et al., 2014). Another 'major transition' that involves an apparent increase in adaptive complexity is the rise of eusociality in insects, including many species of bees, wasps, and ants (Hölldobler and Wilson, 2008; Keller, 1999; Maynard Smith and Szathmáry, 1995).

However, just because combining organisms into groups allows for higher levels of adaptation to evolve at the group level, this does not mean that higher levels of adaptation actually *will* evolve. After all, some members of a group may be adapted to exploit other group members, as in interactions between hosts and parasites, or between predators and prey. A group characterised by antagonistic interactions of this sort is very unlikely to achieve a high degree of group-level adaptation.

These considerations suggest that, in addition to facilitating the study of adaptation in individual organisms, the adaptation measure proposed here might also facilitate research on the units of selection and on major transitions in evolution. For example, the adaptation measure may make it possible to unambiguously identify the period of evolutionary history when selection becomes effective at a higher level of biological organisation (i.e., when a superorganism emerges). This could be done by simply recording a group-level adaptedness measure over time. If the adaptation measure undergoes a substantial and long-lasting increase in value, then we have evidence for the emergence of individuality at a higher level of biological organisation (Michod and Roze, 1997; West et al., 2015). That is to say, we have evidence for the emergence of a superorganism.

What could lead to the emergence of a superorganism? A number of different mechanisms are possible. However, one important group of mechanisms involves factors that reduce (or eliminate) the effectiveness of individual selection with groups. Mechanisms of this sort include monogamy, which reduces competition for mates, and 'policing' to ensure that 'selfish' behaviours are unprofitable. Another mechanism is the use of very small population numbers during the founding of new groups. This tends to reduce within-group variation, and thus it causes a decrease in the effectiveness of within-group selection (Michod and Roze, 1997; Peck and Feldman, 1988; Ratcliff et al., 2015; West et al., 2015).

Acknowledgements

We thank Andy Gardner, Richard Neil, and John Welch for insightful comments. In addition, we are grateful for support from the Centre for Computational Systems Biology at Fudan University, and from the Department of Genetics at the University of Cambridge. This article is dedicated to the memory of Shulamit Peck, a true Woman of Valour.

Appendix A. Adaptedness associated with randomly assigned organismal types

In this appendix we investigate the properties of adaptedness, when the fitness of different organismal types are randomly assigned.

Overview

Let $w_1, w_2, \ldots, w_\Omega$ be the relative fitnesses of different organismal types of a comparison set of size Ω. The adaptedness of type j is given by $\alpha_j = \log_2(\frac{\Omega}{Q_j}) = \frac{1}{\ln(2)}\ln(\frac{\Omega}{Q_j})$ where Q_j is the number organismal types with relative fitness $\geq w_j$. We shall independently draw all w_j from a continuous probability distribution, so all w_j will be different from one another. We show that the ratio Q_j/Ω takes the values $1/\Omega,\ 2/\Omega,\ \ldots, \Omega/\Omega$ with equal probability (namely $1/\Omega$). For large Ω ($\Omega \gg 1$), we can, for many purposes, approximate this discrete distribution by a uniform probability distribution over [0, 1]. Under this approximation, the adaptedness, α_j, has an exponential distribution with parameter $1/\ln(2)$ such the mean and standard deviation of α_j are both equal to $1/\ln(2)$.

Details of calculation

To begin, we write $Q_j = \sum_{k=1}^{\Omega}\theta(w_k - w_j)$ where $\theta(x)$ is 1 for $x \geq 0$ and 0 otherwise. We imagine repeatedly drawing all Ω of the w_j at random from a common probability distribution. The set of α_j values obtained by this procedure can be viewed as realisations of a random variable and their distribution (probability density) summarises the statistical properties of the α_j.

Proceeding, we introduce the quantity $R_j = Q_j/\Omega$. Under the repeated independent drawing of all Ω of the w_j, the values of R_j can also be treated as realisations of a random variable. Relevant results for R_j follow from its characteristic function, which is defined as $C(\lambda) = E[e^{i\lambda R_j}]$ where $E[\ldots]$ denotes independently averaging over all w_j from a common distribution.

We have $C(\lambda) = E[e^{i\lambda R_j}] = E[e^{i\lambda\sum_{k=1}^{\Omega}\theta(w_k - w_j)/\Omega}] = E[e^{i\lambda\theta(0)/\Omega + i\lambda\sum_{k=1(k\neq j)}^{\Omega}\theta(w_k-w_j)/\Omega}]$. This can be written as $C(\lambda) = e^{i\lambda/\Omega}E_j[(E_k[e^{i\lambda\theta(w_k-w_j)/\Omega}])^{\Omega-1}]$, where $E_k[\ldots]$ denotes averaging only over w_k. With $\varphi(w)$ denoting the common probability density of the relative fitness of a single organismal type, we have $E_k[e^{i\lambda\theta(w_k-w_j)/\Omega)}] = \Phi(w_j) + e^{i\lambda/\Omega}[1 - \Phi(w_j)]$ where $\Phi(w) = \int_0^w \varphi(w)dw$. Thus $C(\lambda) = e^{i\lambda/\Omega}\int_0^1 (\Phi(w_j) + e^{i\lambda/\Omega}[1 - \Phi(w_j)])^{\Omega-1}\varphi(w_j)dw_j$. Assuming that $\varphi(w)$ is a continuous function of w we write $\Phi(w_j) = x$ and have $\varphi(w_j)dw_j = dx$. We thus find that independent of the form of $\varphi(w)$, $C(\lambda) = e^{i\lambda/\Omega}\int_0^1 (x + e^{i\lambda/\Omega}(1-x))^{\Omega-1}dx$, i.e., $C(\lambda) = e^{i\lambda/\Omega}\frac{1-e^{i\lambda}}{\Omega(1-e^{i\lambda/\Omega})}$. This characteristic function of $R_j = Q_j/\Omega$ corresponds to R_j having a discrete uniform distribution where it takes each of the values $1/\Omega,\ 2/\Omega,\ \ldots, \Omega/\Omega$, with probability $1/\Omega$. The $\Omega \to \infty$ limit of this distribution is the standard uniform distribution where R_j is uniformly distributed over [0,1] and for this case we shall write $R_j = U$ where U is a standard uniform random variable. As a consequence, for very large Ω we can approximate the adaptedness as $\alpha_j = -\ln(U)/\ln(2)$, and this corresponds to a random variable with an exponential distribution with parameter $1/\ln(2)$:

$$\alpha_j \sim Exp\left(\frac{1}{\ln(2)}\right). \tag{A1}$$

We note, in particular, that the expected value of α_j and its standard deviation both have the value $1/\ln(2) \approx 1.443$.

Appendix B. Independence of relative adaptedness on the size of the comparison set

We show that the difference in the values of adaptedness of two particular organismal types is unchanged when the size of the comparison set is increased, due to the addition of organismal types which have lower relative-fitness values than those associated with the particular two types.

Consider a comparison set for which types i and k have adaptedness values $\alpha_i = \log_2(\frac{\Omega}{Q_i})$ and $\alpha_k = \log_2(\frac{\Omega}{Q_k})$, respectively. We construct a new comparison set by adding organismal types that are *less fit* than both organismal type i and organismal type k, with the new comparison set having $\breve{\Omega}$ organismal types. On calculating the new adaptedness values for the larger comparison set, the values of Q_i and Q_k remain unchanged (since these are independent of the number of organismal types with relative fitnesses *lower* than those of type i and type k, respectively). Thus the new adaptedness values are $\breve{\alpha}_i = \log_2(\frac{\breve{\Omega}}{Q_i})$ and $\breve{\alpha}_k = \log_2(\frac{\breve{\Omega}}{Q_k})$ and the difference is $\breve{\alpha}_i - \breve{\alpha}_k = \log_2(\frac{Q_k}{Q_i})$. We also have $\alpha_i - \alpha_k = \log_2(\frac{Q_k}{Q_i})$. Hence $\alpha_i - \alpha_k = \breve{\alpha}_i - \breve{\alpha}_k$, independent of the size of the comparison set.

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