

# The Price Equation and Reproductive Value

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December 6, 2019

Keywords:

reproductive value

fitness

Fundamental Theorem of Natural Selection

Secondary Theorem of Natural Selection

Price Equations

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## Abstract

The Price Equation is widely recognised as capturing conceptually important properties of natural selection, and is often used to derive versions of Fisher’s fundamental theorem of natural selection, the secondary theorems of natural selection, and other significant results. However, class structure is not usually incorporated into these arguments. From the starting point of Fisher’s original connection between fitness and reproductive value, a principled way of incorporating reproductive value and structured populations into the Price Equation is explained, with its implications for precise meanings of (two distinct kinds of) reproductive value and of fitness. Once the Price Equation applies to structured populations, then the other equations follow. The fundamental theorem itself has a special place among these equations, not only because it always incorporated class structure (and its method is followed for general class structures), but also because that is the result that justifies the important idea that these equations identify the effect of natural selection. The precise definitions of reproductive value and fitness have striking and unexpected features. However, a theoretical challenge emerges from the articulation of Fisher’s structure: is it possible to retain the ecological properties of fitness as well as its evolutionary out-of-equilibrium properties?

## 1 Introduction

Queller (2017) extends the term ‘fundamental theorem’ beyond Fisher’s original to some four further well-known results, namely the Price Equation as the most fundamental, with Fisher’s average excess equation, the secondary theorem of natural selection, the breeders equation, and Fisher’s original as deriving from it, with the remark that ‘Each highlights a particular core issue of evolution’ (page 348). Queller’s links and versions of the theorems all involve unstructured populations, in which all individuals are equal. The current paper shows how the Price Equation is extended to structured populations and environmental uncertainty. Fisher’s original theorem was for an age-structured population, and it is by generalising his approach that other class structures are included. This leaves Queller’s valuable anatomy of results unaltered, but draws attention to three important points. Fisher’s original theorem will turn out to have a special role in defining natural selection, and so perhaps especially deserving of the term ‘fundamental theorem of natural selection’. The terms ‘reproductive value’ and ‘fitness’ are widely used in biology, and the introduction of class structure has important implications for their inter-relationships and meaning. The principled approach to natural selection by operating through these high-level equations leads us to expect that natural selection will cause organisms to maximise their expected fitness, with implications for the concept of bet-hedging.

The immediate problems posed by class structure are that fitness becomes hard to define, as one's descendants next year may be in different classes (surviving self vs newborn; daughter vs son), and that natural selection becomes harder to define (as gene frequencies can go in different directions in different classes). The question of whether fitness-maximisation ideas can survive in this more complex world comes down to: what is our definition of fitness? how do we decide how much of an evolutionary change should be attributed to natural selection? and finally, does natural selection increase fitness? The whole point of Fisher's fundamental theorem is to answer the first two questions with definite proposals, generalisations of which are employed in this paper, and then to provide a resounding "yes" to the third. The concept of reproductive value is key to defining fitness and to measuring natural selection, and to defining fitness.

The terms fitness and reproductive value are much used in biology. Their various different definitions, and uses without precise definitions, embody the variety of biological research. However, the definitions required to make these fundamental theorems work have a special claim on us, and biologists should use them wherever possible, and teach them to their students. The purpose of the current paper is to present verbally important points that have emerged in highly mathematical papers - readers seeking a mathematical exposition are referred elsewhere (Grafen, 2015a,b; Batty et al., 2014; Crewe et al., 2018), though some of the points below represent more recent advances in understanding.

Before making a start, the reader should be aware that this paper will consider Fisher's idea of fitness, and not extend to social behavior through the inclusive fitness of Hamilton (1964): while that would be desirable, the incorporation of inclusive fitness into the general body of theory is insufficiently advanced. A further preliminary is that we will usually discuss overlapping generations in discrete time. A 'year' will be used as the basic unit of time, so that an individual survives or not from one year to the next and has a certain number of offspring in a given year, and we don't keep track of finer time divisions.

Finally, writing this paper to articulate in words the roles of reproductive value and fitness has greatly improved my own understanding of the logical connections between the ideas in Fisher's ingenious construction, and I hope reading it may help others. Lion (2018a) has recently written very usefully on the nature of reproductive value. He explores in non-equilibrium situations the requirement (here called 'neutrality') that in the absence of selective forces, gene frequencies do not change, building on a literature (Rousset and Ronce, 2004; Rousset, 2004) that achieves this through reproductive-value weighting, but without any connection to a central theme of the present paper: the connection between reproductive value and fitness. Lion's model has technical differences, including allowing total population reproductive value to change over time, and

not indexing over individuals, and it is also restricted to clonal reproduction. For interesting new uses of reproductive value in relation to the Price Equation, see Lion (2018b).

## 2 Basic, Williams', and fitness

The basic reproductive value is simply a number for each demographic class in a given year that represents the relative evolutionary significance of one haploid set of genes. Each individual has a reproductive value equal to the sum of the reproductive values of its haploid sets (thus, its ploidy times the class-based reproductive value), and a whole class has a reproductive value found by summing (*not* averaging) the reproductive values of all individuals in the class. The basic reproductive values may be the same next year, but sometimes they may well turn out to be different. We will rather loosely refer to per-capita reproductive values when we mean per-haploid-set, and will intend the per-capita values unless *total* is explicitly mentioned. Fisher defined his reproductive values to be constant over time, which is convenient for some purposes, but it will be important to understand that change over time is possible and likely. For the moment, the reader is asked to continue with the Price Equation approach, which is to accept for the moment that the reproductive values are arbitrarily assigned as nonnegative numbers, on the promise that we will return to how they are calculated.

A second kind of reproductive value was introduced by Williams (1966), in the founding paper of life-history theory, and which has since often been used under the label 'fitness'. Under the impression that this quantity was what Fisher had shown individuals maximise, Williams defined the new kind of reproductive value as follows. An individual may or may not survive to the next year. The first part of her Williams' reproductive value equals the chance that she does survive multiplied by the basic reproductive value of the class to which she will then belong (i.e. one year older, with a simple age structure). The second part equals her share of the summed basic reproductive values of the offspring she can expect to produce in that year. Her share would be a half under sexual diploidy. The basic reproductive value of the offspring would be that for a newborn. This therefore uses the basic reproductive values next year to calculate a new reproductive value for each individual this year. Note that this 'Williams' reproductive value' is not in general the same for all individuals in the same class. Indeed, the possibility of natural selection depends on genetic variation causing differences in Williams' reproductive value; but environmental and chance events will also make individuals in the same class have different Williams' reproductive values. Williams' reproductive value is an exercise in counting expected number of gene copies, weighting by the simple reproductive

values.

Frank (1998, 2012) explains the Price Equation as employing a special kind of indexing of the offspring generation. The individual's Williams' reproductive value embodies this indexing, so that offspring are counted as belonging to a parent according to the fraction of their own basic reproductive value that contributes to the parental Williams' reproductive value.

The final concept to be defined in this section is fitness. Williams' reproductive value is used in life history theory as a maximand. Individuals are expected to make choices that lead to the greatest possible Williams' reproductive value at each moment in time. Indeed, some authors do use Williams' reproductive value and call it fitness, but recent work has revealed what Fisher meant by fitness in his fundamental theorem of natural selection (Grafen, 2015a, but see Section 4.4 for an alternative). In discrete time, we can think of fitness as the Williams' reproductive value divided by the individual's basic reproductive value. Maximising Williams' reproductive value is the same as maximising fitness, because the basic reproductive value is taken as given. This division does something very interesting: it makes the mean fitness equal in every class. Why this is and why it matters will be explained in Section 3.1.

(To match the continuous time version of fitness as closely as possible, we would here define fitness as the Williams' reproductive value minus the basic reproductive value, divided by the basic reproductive value. This makes the mean fitness of a stationary population equal to zero, whereas the definition without the subtraction makes the mean fitness equal to one. There are no serious differences between these definitions and, in view of the substantive equivalence, the easier to understand has been adopted. Stability in biology is often associated with a value of 0 in continuous time and of 1 in discrete time.)

Fitness has some surprising properties under this definition. It is not a single 'tombstone evaluation' of an individual's evolutionary success. Rather an individual will have a fitness at each moment in time, and it counts future reproduction only, and relative to class expectations. Fitness measures how well you do at future spreading of your genes compared to how well an average individual in your situation does.

## 2.1 The temptations of anticipation

The definitions of basic reproductive value, Williams' reproductive value and fitness, as just set out, hold good within a wide class of models, as we shall see. There is an obvious temptation to 'improve' the definitions by trying to value offspring according to their own individually variable successes, rather than in terms of the basic reproductive value which is the same for all members of the class to which they belong. This temptation will in some cases have biologically valid underpinnings, and this subsection considers those cases. However, the

conclusion will be that anticipation is generally a bad idea.

If we are interested in the grandmother hypothesis (Williams, 1957), for example, clearly we need to capture in measuring one individual's evolutionary success its number of grandoffspring, and perhaps even the number of offspring those grandoffspring themselves have. This is not captured in the formal structures on which the definitions proposed are based, and so the urge to break the structure is understandable. These transgenerational effects are complicated to model, and interested readers are referred to Lehmann (2007) for the best treatment of it to date, though the model has no demographic structure. The basic reason not to move to grandoffspring as a measure of fitness in general is that a model works only because it has a simple structure, in which the demographic classes capture the important differences between individuals. Once you give each individual a name, and know their whole family tree, there are two problems. One is no longer doing science, but gossiping about acquaintances, and further there is no natural place to stop. If grandoffspring, why not greatgrandoffspring, and so on? It is unsatisfactory to rely on the indefinite future, because all lineages will go extinct, and recognising this would make every current reproductive value equal to zero. Sex ratio theory is often explained in terms of counting grandoffspring, but this only is a convenient fudge, to avoid needing the concept of reproductive value. A principled way to study sex ratio (e.g. Fisher, 1930; Boomsma and Grafen, 1991) is to recognise males and females as demographic classes, and then to calculate their reproductive values. As Fisher first noted, the total reproductive values of males and females are equal under diploidy (but see Goodman, 1982; Grafen, 2014, for a qualification), and so the per-capita reproductive values are inversely proportional to the number of males and females, and this gives the required frequency dependence in one generation, without having to consider grandchildren. Creating demographic classes in order to look only one generation ahead will usually be the right solution – of course, in calculating the reproductive values, we will in a sense be looking further ahead, but in way permitted by our underlying model, and not on an individual-by-individual basis.

A second reason for temptation is to do with genetics. If I have an advantageous allele, then I will do well, and my offspring will tend to possess that allele more than the population at random. Should we not recognise that, by incorporating their success into my reproductive value? Again, we have a problem of consistency. If the allele will go to fixation or extinction, then by counting far enough ahead we will give all individuals today a high reproductive value if they possess the allele and zero if they don't. Some (e.g. Kimura, 1958; Crow, 1979) suggested defining fitness based on genotype and not on age, but Grafen (2015a) argues that this was not Fisher's intention, which is the focus of the present paper. We therefore continue with the approach of defining reproductive

value and fitness with no explicit dependence on genotype.

Another point to consider beyond consistency, which applies to grandmothers and genetics, is that we would like the measure of fitness, once calculated from the reproductive values, to measure the effect of one individual's actions on the success of that individual's genes. If we count ahead on the basis of shared alleles, then we are placing into one individual's fitness the effects of all the descendants' actions too. If we do the same for the descendants in a generation or so's time, we will be exaggerating the strength of natural selection by double or triple counting, or worse. The structure of demographic classes and their reproductive values is set out in order to consider the relationship between fitness and genotypes, which will illuminate natural selection. Second-guessing aspects of natural selection interferes with this structure, and needs an explicit mathematical justification.

A general reason for not bringing forward all the events in future generations is that our purpose in calculating fitness is to study natural selection at one moment. The fitnesses of the next moment will be relevant to natural selection in the next moment. Bringing events forward would be right if we were trying to study the total effect of natural selection over all generations. Unless we are trying to do that, and have set up a whole analytical framework consistently to achieve that goal, we should allow the cares of the day to be sufficient to the day thereof.

Thus, there are biologically understandable motivations for anticipation. However, they do lead to paradox, and should usually be avoided. Some kinds of actions do lie outside the scope of the models within which reproductive value and fitness are defined, as currently being suggested, and these should of course be recognised and given special treatment. One formal treatment of anticipating reproductive value is by Barton and Etheridge (2011), but their assumptions, specifically of weak selection, reduce the impact of multiple counting. A recent empirical paper by Reid et al. (2019) considers how to measure fitness in a field study with enough long term data to incorporate anticipation if desired.

The major point to emerge from this section is that evaluating the effect of natural selection is a technical business, and the structures set out for this purpose are generally not improved by informal embellishment.

## 2.2 From one generation to the next

Two complete sets of basic reproductive values have appeared so far, namely the reproductive value of each class this year, and the reproductive value of each class next year. The basic values from next year are used to calculate the Williams' reproductive values for this year. Nothing we've said so far forces any connection between the two sets of basic reproductive values. However, there is one central obligatory property that operates by connecting two successive

sets of values. This will allow many of the important properties of the concepts to be exhibited. In a later section, we will finally pin down both sets of values by invoking *iteration*, that is, requiring that the one-generation-to-the-next connection holds not just this year, but in all subsequent years as well.

There are two ways of envisaging how reproductive values should be connected across the generations, and they will turn out to be equivalent. Demographically, it seems sensible that an evolutionary valuation of a class should be equal to the sum of its share of the reproductive values of the classes next year, where the appropriate share is the fraction of the genes in that class next year that derive from genes in our focal class this year.

The other way to connect reproductive values across the generations is to remember that the reproductive values affect how we average class gene frequencies to work out the population gene frequency, and that we measure natural selection as a change in population gene frequency. The property that reproductive values produce no change in population gene frequency in the absence of selection has been important for some time (not begun but formalised by, e.g. Taylor, 1990, 1996; Rousset, 2004), and Grafen (2015a,b) proposed elevating it to be the defining property. Thus, the neutrality requirement is that the reproductive value weights should be chosen so that the weighted population mean gene frequency does not change in the absence of natural selection – see Section 3.1.

The important point of principle is that the demographic and neutrality requirements turn out to be the same, so that adopting one is equivalent to adopting the other. If we fix the reproductive values for next year as arbitrary nonnegative numbers, then either criterion defines the reproductive value this year. The other way round does not necessarily work, and it will later be important that we always work backwards with reproductive values, assuming we know a future set, and then calculating what the current set must be.

In defining reproductive values, we require that they work for all possible initial sets of class numbers, or for all possible sets of initial gene frequencies. This implies that the properties they give rise to hold whether or not the population is in demographic equilibrium.

A number of important consequences follow from ensuring that the reproductive values for this year and next year satisfy the one-generation-to-the-next requirement. First, the total reproductive value of the population remains constant over time, as the sum of the reproductive values this year equals the sum of the reproductive values next year. A second important implication is that the mean fitnesses of all the classes are equal, and are equal to one, and it is easy to see why. The demographic version of the one-generation-to-the-next requirement says that the total basic reproductive value of class  $x$  equals the sum of the fractions of the basic reproductive values of the classes next year that derive



from class  $x$  this year. However, the first of these quantities equals the sum of the basic reproductive values of individuals in class  $x$ , and the second equals the sum of the Williams’ reproductive values of the same individuals. As the individual basic reproductive values within a class are all equal, it follows that the average Williams’ reproductive value equals one. This argument applies to each class. Fisher did not reach this conclusion because he allowed proportionality, and specifically did not require equality, in the one-generation-to-the-next requirement that supplies the premiss of the current argument. (See Lemma 2 on page 1080 of Crewe et al., 2018, for a mathematical version of the second point).

The conflict with Fisher’s own definition of fitness, in which the mean fitness of each class is the Malthusian parameter, will be further explained in Section 4.3 – there is no real discrepancy. What matters in the next section is the consequences of all the fitness class means being equal for the interpretation of the Price Equation, and not what the shared value is.

### 3 The Price Equation and fundamental theorem

The Price Equation is a widely known and well-studied result in evolutionary biology, recognised by Queller (2017) as the logical progenitor of the other formulae he discusses, and there are many introductions and explanations (e.g. Frank, 2012). Our purpose here is to use it to define natural selection in the presence of classes, and as this requires weighting individuals following the advice of Fisher (1930) we need to use the equation of Price (1972a) rather than the simpler version of Price (1970). In 1972, the trait whose mean change is expressed has become any trait, not necessarily connected to genetics, indeed the equation is described as about selection in general, whether of candidates for a post, candidates in an election, or aphids selected by a ladybird for eating. However, for our purposes we will assume that trait is still a gene frequency (or weighted sum of the individual’s gene frequencies).

The 1972 Price Equation discusses a change between two weighted averages, where the both the underlying traits and the set of weights may be different between the two averages. Here, we stick to the same underlying trait, namely a gene frequency (or weighted sum of gene frequencies) in the parental generation. The first set of weights will be the basic reproductive values, and so the first average is the gene frequency in the parental generation; while the second set will be the Williams’ reproductive values, and so the second average will be the gene frequency in the offspring generation, even though the average is taken over the parental generation. The Williams’ reproductive value has been defined to make this equivalence hold good.

We write the gene frequency of individual  $i$  as  $p_i$ , and the basic and Williams’

reproductive values as  $w_i$  and  $w'_i$ . Within statistical operators, the subscript will be omitted to make for easier reading, again following Price (1972a). So,  $\text{ave}_w p$  is the gene frequency in the parental generation, weighting by basic reproductive value, and  $\text{ave}_{w'} p$  is a weighted sum of the same parental gene frequencies, but weighting by the Williams' reproductive values. We intended the Williams' reproductive values to be a measure of how many gene copies were on average placed in the population next year, and so  $\text{ave}_{w'} p$  should be the gene frequency next year. Further notation is that  $s_i = w'_i/w_i$  is the fitness of individual  $i$ , and  $\tilde{s}_i = s_i/\text{ave}_w s$  is that fitness relative to the reproductive-value-weighted population mean. Although we have argued that the mean fitness equals one, and  $s_i = \tilde{s}_i$ , we continue with relative fitness for consistency with Price's treatment. Recalling the definition of covariance, we can repeat it for clarity with weighted values, so that  $\text{cov}_w(a, b) = \text{ave}_w(ab) - \text{ave}_w(a)\text{ave}_w(b)$ . Now we can state Equation (A 12) of Price (1972a), which is

$$\Delta(\text{ave}_w p) = \text{cov}_w(\tilde{s}, p) + \text{ave}_{w'}(\Delta p).$$

The left-hand-side notation is shorthand for  $\text{ave}_{w'} p' - \text{ave}_w p$ , and is therefore the difference in reproductive-value-weighted gene frequency from this year to next. This weighting gives the appropriate measure for assessing natural selection. The right hand side comes in two parts. The first is a covariance across individuals between relative fitness and gene frequency. Note that the same individual fitness would apply, whichever gene's frequency we are considering. This term can be regarded as the part of the change that is due to natural selection at the individual level, as it comes from a link between individual gene frequency and individual fitness – however, we will see below that Fisher's fundamental theorem is the proof that this interpretation is a good one. The second term is about how the genes an individual passes on are not representative of the individual's own genome, and  $\Delta p_i$  measures that difference. The term includes effects of phenomena that we can list from less to more exotic: the randomness of Mendelian segregation, mutation, and gametic selection and meiotic drive. It will sometimes be reasonable to average over Mendelian segregation (when we're not interested in genetic drift), and to assume there is no mutation, gametic selection or meiotic drive, when we are focussing on the effects of individual natural selection.

A Price Equation contains within it the seeds of a fundamental theorem, about whose logic and history Edwards (1994, 2002, 2014) makes important points. Taking the Price Equation, the first step is to assume that the second right hand term is zero, which involves assuming no mutation, no meiotic drive and no gametic selection, and also a population large enough to render negligible the net effect of the randomness of Mendelian segregation. Remember  $p_i$  can be not just a single gene frequency, but any weighted sum of gene frequencies, and

we choose  $p_i$  to equal the breeding value of fitness. Breeding value is the best additive genetic guess at fitness, calculated in principle statistically from the genotypes and fitnesses of individuals in the population – for technical details of the calculations in general, see Lynch and Walsh (1998), and for this example see Grafen (2015b, and note that the regressions providing breeding values must themselves be weighted by reproductive value). The consequence is that the left hand side of the Price Equation becomes, in Fisher’s interpretation (which is supported by Grafen (2018) though disputed by Lessard and Ewens (2019)), the part of the change in mean relative fitness that is due to natural selection. The right hand side equals the covariance between the breeding value of relative fitness and relative fitness itself, and standard arguments (Lynch and Walsh, 1998) show that this equals the additive genetic variance in relative fitness. Thus, the fundamental theorem here says that

The part of the change in mean relative fitness that is due to natural selection is equal to the additive genetic variance of relative fitness.

Grafen (2015a, 2018) argues that the importance of the theorem is that it shows natural selection to be an improving process, because its contribution to the change in mean relative fitness is positive; that other forces may well be having negative effects at the same time, and indeed the mean of relative fitness must always equal 1, so any positive effect of natural selection *must* be counterbalanced to produce a net change of zero; and as confirming that the way fitness is measured is an appropriate way of measuring whatever it is that natural selection improves. The Price Equation therefore measures the effect of natural selection on every gene frequency, and on the breeding value of any trait, while the fundamental theorem measures natural selection in its totality as the additive genetic variance in relative fitness. However, recall that we have not fully defined the reproductive values, only specified that they should be subject to the one-generation-to-the-next property of Section 2.2. It is interesting to consider that both the equations hold whatever non-negative choices we make for next year’s reproductive values.

The one-generation-to-the-next property assures us that changes in mean trait attributed by the Price Equation to natural selection, or increases in mean fitness ascribed by the fundamental theorem to natural selection, are not caused by ‘passive’ changes through class inheritance. This is the main purpose of that property, and we now consider two examples of the danger that is avoided by adopting it.

### 3.1 Examples and general case

We begin with two simple examples, and then give the abstract argument to the same end, that weighting by reproductive value avoids counting ‘passive’

changes in gene frequency towards the effect of natural selection. First, the iterated version will be explained, even though that anticipates a later section, as it is a simpler way to get the main point across. Then the current point will be made, that we are free to choose reproductive values for next year, which allows us to calculate reproductive values for this year, and that combination will provide no evolutionary change.

In the simplest nonsocial haplodiploid breeding system, each year females and males emerge in the spring. They mate and produce young, which overwinter. The two demographic classes are females and males, and the question is what are their total reproductive values? If we know the gene frequency in females, say  $\pi_f$ , and that in males, say  $\pi_m$ , how should we produce an overall gene frequency  $\pi$ ? Consider an allele with the extreme distribution that all females are homozygous for that allele, while males do not possess it, in the starting generation. Then without selection in a very large population we can calculate that the gene frequencies change over time as  $(1, 0)$ ,  $(1/2, 1)$ ,  $(3/4, 1/2)$ ,  $(5/8, 3/4)$  and so on. The rule is that the female frequency equals the (unweighted) average of the females and males of the previous year, while the male frequency simply equals the female frequency of the previous year. The complementary allele would have frequencies  $(0, 1)$ ,  $(1/2, 0)$ ,  $(1/4, 1/2)$ ,  $(3/8, 1/4)$  and so on. We require weights that ensure the overall population gene frequency does not change over the years. It turns out that (only!) weights of  $(2/3, 1/3)$  do the trick, so that frequency of the first allele starts at  $2/3$  and remains there, while the frequency of the second allele starts at  $1/3$  and remains there. The total reproductive values of females and males are therefore proportional to  $2/3$  and  $1/3$ .

We can also look not at the iterated system, hoping to find consistency across a number of years, but just at pairs of years at a time, in keeping with the one-generation-to-the-next principle of the previous section. Suppose then that we choose total reproductive values for next year of  $f$  for females, and of  $1 - f$  for males. It follows that this year's females must have a reproductive value of  $(1 - f/2)$ , as this is all the male value from next year and half of the female value. This leaves  $f/2$  for this year's males. The weighted average for the first year's gene frequencies  $(1, 0)$  considered as 'this year' is  $1 - f/2$ , and the average for the second year  $(1/2, 1)$  considered as next year is also  $1 - f/2$ . The reader can check that each successive pair of years gives the same gene frequency using this year's weights for the earlier year, and next year's weights for the later year. But the successive frequencies are  $(1 - f/2)$ ,  $(1/2 + f/4)$ ,  $(3/4 - f/8)$ ,  $(5/8 + f/16)$ , and so on. Thus, there is no change in frequency between pairs of successive years with this weighting, but there is change on any one weighting over the sequence of years. Only by choosing  $f = 2/3$  do we find that all the year's averages equal  $2/3$ . The surprising feature is that only the

‘pairs of years’ condition is needed to derive many of the properties of fitness.

A second, age-structured, example can be given (Grafen, 2015a). Suppose an age-structured population is found in an unusual genetic situation. All prereproductive individuals have one genotype ( $AA$ ), all reproductive individuals have another ( $BB$ ) while postreproductive individuals have a third ( $CC$ ), and we assume that this locus causes no phenotypic differences. The  $C$  allele is doomed to extinction, while initially  $B$  will be increasing. The new genotype  $AB$  will arise when the currently nonreproductive individuals do begin to breed. In taking population gene frequencies, a special set of weights is required if we insist that the population gene frequency should not change over time. Post-reproductive ages should certainly have zero weighting, and the other ages need exact weights to ensure no change. Those weights will be the reproductive values.

The general point begins with noting that the natural selection term of the Price Equation is a covariance between the gene frequency and relative fitness. If there are genetic differences between classes, perhaps because of recent selection that has now stopped, then any differences in the mean relative fitness across classes would produce a non-zero covariance, as class would be acting like a ‘third variable’ or ‘confounding variable’ in a statistical analysis. The only way to prevent class differences in gene frequencies from automatically creating a non-zero covariance is to ensure that the class means of relative fitness are all equal. This is the significance of the equal class means property. The implication is that natural selection happens within classes, by some genotypes performing better than others, but that differences between classes cannot constitute natural selection.

The same point arises in an even stronger form in the fundamental theorem. If there were genetic differences between age classes, and if hypothetically there were mean fitness differences between age classes, then the fundamental theorem would find that the breeding value of fitness had non-zero variance, and that there was therefore selection going on, even if the genetic differences had no effect on fitness within any age class. Only by ensuring equal mean fitness for the classes can it make sense to attribute the additive genetic variance of fitness to natural selection. Thus, the fundamental theorem and the Price Equation, which biologists use to define natural selection, require the equal-class-mean property to hold for fitness, and this in turn requires choosing reproductive values to satisfy the one-generation-to-the-next condition. Thus, there is a general requirement for our formulations of natural selection that fitness should be defined so that the mean fitness of each class is the same. (Under uncertainty, a question arises that is too technical to be dealt with in this paper: does the equal class mean condition apply to the realised values of fitnesses, or just to the expectation?)

## 4 Iteration

To apply the one-generation-to-the-next condition, we chose non-negative values for next year, and then the condition told us what this year's reproductive values should be, and this gave us the Price Equation and the other formulae. *Iteration* simply says that we should pick reproductive values in five years' time, or ten or a hundred years' time, or a few thousand years' time, and then work all the way back to now. The main phenomenon is one of 'smearing', which is discussed before looking at different ways of iterating. The main outcome is that the further we look ahead, the more closely determined are our current basic reproductive values, and in the limit they are exactly determined.

The concept of smearing is known more mathematically as 'ergodicity', and is well-known to biologists. Take an age structured model, and begin with a population all aged 1. Next year, they will be aged 2, and so on, until the age of first reproduction is reached. Then, there will be some newborns as well, who will continue to appear. The spike of adults at the right edge of the distribution will march onwards, suffering attrition as it moves, but once the smearing has begun, it continues. Eventually, no sign of the original spike exists, and it will be impossible to say in which year the population began with all 1-year olds. Under standard assumptions (which we do *not* generally adopt here, but which will be explained and considered in the next section), the asymptotic age distribution is approached. This smearing happens forwards, to the age structure, but let us see how it also happens backwards, to reproductive values.

Consider the same population in some long-distant future generation, and pick one gene, say in a 33-year-old. One year previously, it must obviously have been in a 32-year old. But when go back 33 years, and the bearer reaches the age of 0, the gene might have come from a range of ages in the previous year, and the probability it came from different ages immediately spreads out over all the reproductive lifespan. This is an important stage in the smearing of reproductive values, but this is not yet the final stage. Just before the year in which the original bearer was born, the gene cannot be found in a pre-reproductive individual. But after a few more years under the same standard assumptions, the reproductive values will settle down to equilibrial values.

This situation provides reproductive values as the foundation for the framework leading to the Price Equation, and readers willing to take on trust further details of how iteration works are encouraged to skip to Section 4.2. But in iterating over years, we have to ask, what will those years be like?

### 4.1 Years differ

The standard assumption is that the projection matrix remains constant over time. The projection matrix's elements say how many offspring in class  $y$  are

produced by the average parent in class  $x$ , for all combinations of classes  $x$  and  $y$ : the most familiar example is the Leslie matrix (Leslie, 1948) for age-structured populations, where the nonzero terms are survivorships and fertilities. In this section, we consider varying that assumption, but also adding environmental stochasticity and density dependence. The now-standard mathematical results (e.g. Caswell, 1982) for the constant projection matrix make the equilibrium class distribution the leading right eigenvector of the projection matrix, and the reproductive values its leading left eigenvector. So, a constant projection matrix allows these important quantities to be calculated straight away. Now, however, we consider the much more plausible situation of non-constant projection matrices.

The first objection to constant projection matrices is the implication that there is no density-dependence. As the population grows, surely birth rates should come down and death rates should go up? Thus the population class distribution may affect the projection matrix. The second objection is that the world is full of variation, and we should really allow random variability in the projection matrix, with possible correlations across years.

Sometimes we don't even want to work with the projection matrix at all. As already mentioned, Fisher began his sex ratio argument by showing that the total reproductive value of females equals that of males under diploidy: this is an argument based on what we may call the 'gene frequency progression matrix', which tells us what fraction of genes in class  $y$  offspring came from parental class  $x$ . This is another matrix that we could in principle decide to assume remains constant over time.

If we know one of these matrices and the numbers in each class, then we can calculate the other matrix: the issue is really which of them is independent of the population class distribution, and which of them depends on it. The only biologically reasonable conclusion is that *neither* matrix is generally independent of the population class distribution. For example, we've already seen that the projection matrix should respond to density dependence, so that survivorships and/or fertilities fall as the population size increases. Apart from the extreme example of sex ratio, it is likely that the fraction of genes contributed to class  $y$  offspring by class  $x$  parents will be higher if there are more parents in class  $x$ . Thus, neither simple assumption should be relied upon.

It is useful at this point to explain that a set of reproductive values can be doubled or trebled without affecting anything important – it is only the ratios of the values that matter. Thus, when below 'uniquely defined' reproductive values are mentioned, the reader should understand that the ratios of the elements are uniquely defined, but multiplication by any positive constant is still allowed. Though note that once the absolute values of one year's reproductive values are fixed completely, the one-generation-to-the-next condition then fixes the

previous year’s completely too.

It is fortunate that the smearing tends to occur even when neither simple assumption is true, and even under randomness with cross-year correlations: it takes very extreme circumstances, such as reproductively non-intersecting subsets of the population, to stop the smearing. To see how reproductive values are affected, let us first note that constant projection matrix or constant gene frequency progression matrix will give us unique reproductive values, and then consider a slightly more complicated and artificial, but very revealing, situation. Suppose that there is a cycle of projection matrices, which repeats every five years: how does the smearing operate then? Rather like multi-period cycles in simple population models, the population approaches a fixed cycle of class distributions that repeats every five years – the initial condition will determine which of the five years it gets into phase with. This leads after a while to a repetition of the same five class distributions, which makes perfect biological sense. There is also a cycle of reproductive values that repeats every five years, which is not so obvious, but true. The exciting fact is that in any one year, we take that year’s reproductive values as our basic reproductive values, we calculate the Williams’ reproductive values using the following year’s reproductive values, and calculate fitness as the ratio of one to the other. This fitness has all the properties discussed earlier, making the fundamental theorem and Price Equations work, along with all the sequelae of Queller (2017), and so characterising natural selection for us in just the same way as under the simple standard assumption of a constant projection matrix.

This artificial cyclic example suggests that in more complicated cases, we would similarly have reproductive values defined in each year. In cases of random environments, the reproductive values might be different depending on the environment, but we could still use them to calculate fitnesses and operate our main equations, and feel they inform us about natural selection. The next section says more about this.

## 4.2 Price Equation with uncertainty

It is good news for the study of evolution that the structure of reproductive value and fitness survives density-dependence and stochasticity, though there are practical implications, notably that class-based schedule of per capita reproductive values will not remain constant over time, specifically it will depend on the environment. The main result to justify this claim in the current context is due to Crewe et al. (2018), and Lion (2018a) makes parallel points about the dynamic nature of reproductive value in the presence of environmental change and density dependence, in his own setting. There is, of course, a kind of stationarity involved, whose foundational centrality will be discussed shortly. Although years may have different environments, and the probability distribution of next



year’s environment may depend on this year’s environment, that structure of dependence is not allowed to change – technically, we have a stationary Markov process over environments. Crewe et al. assume a model with a finite population, but a possibly infinite number of classes. Each class has its own ploidy, and the numbers of offspring that each individual produces is allowed to be random, and to depend on the environment this year as well as on the state of the population (i.e. how many individuals there are in each class). The nature of reproductive values is defined, but it is not proved in general that they exist (for reasons to be discussed later), though they are likely to in most biologically plausible models. If they do exist, then each individual has a basic reproductive value and a Williams’ reproductive value, and a fitness as the ratio, just as in the simpler cases. The major result is that this individually-defined fitness allows a Price Equation to be written. By incorporating fair Mendelian segregation into the randomness of the environment, and assuming no mutation, gametic selection or meiotic drive, we obtain

$$\mathbb{E} [\Delta(\text{ave}_w p)] = \text{cov}_w (\mathbb{E} [\tilde{s}], p) .$$

This equation is the same as the deterministic version, except that in a random model, we link the *expected* change in the frequency of any allele, with the covariance between the individual’s allele frequency and the individual’s *expected* fitness. It is useful to find a result in which the only difference from the deterministic case is that the random terms are replaced by their expectations. There is also, as you would expect, a version of Fisher’s fundamental theorem, but there is no space to explain it here.

Of course, this recognises that studying natural selection under varying environments is complicated, and there would be problems to overcome in applying these ideas in an empirical example. But it is important that in principle our structure of reproductive value and fitness, and Queller’s main evolutionary equations, survive intact under plausible biological assumptions. It is also likely that the empirical complications would lead us into biologically significant investigations that really would be important for how natural selection was operating, rather than lead us into pointless complications. This viewpoint, in other words, is more likely to help us out of a mess we didn’t realise we were already in, than to create new and unnecessary problems.

There are technical limitations to the Crewe et al. paper, which they discuss, along with comparisons of this result with the uses of reproductive value by Tuljapurkar (1989) and Rousset and Ronce (2004) and Rousset (2004), and see also the discussion by Lion (2018a). They also correct previous work that used Williams’ reproductive value as fitness. It is likely the limitations can be relaxed. The possible non-existence of reproductive values arises because mathematical theorems proving existence require simple situations so they can be absolutely

sure. Once the matrices depend on the population state, this goes beyond the scope of the ergodic theorems I am aware of. However, the general power of flattening of matrix products towards a rank of 1 suggests that biologists can reasonably continue these explorations without waiting for formal results on the subject.

One implication will be discussed here. This treatment of uncertainty shows that individuals should be expected to maximise their expected fitness, and in particular they show that the variability in fitness does not affect the expected change in gene frequencies. A whole literature in biology is devoted to ‘bet-hedging’ (see Frank and Slatkin (1990) for a review and technical treatment, and Seger and Brockmann (1987) for more flavour) and authors continue to find that the quantity maximised by natural selection is the mean fitness minus some constant times the variance in fitness (e.g. Lande et al., 2009, 2017). This divergence arises because when fitness is made relative to the population mean, the variance turns out to be irrelevant, while when fitness is defined in absolute terms it is common to find a variance term creeping in (this effect of relativising fitness is explained by Grafen, 1999). Frameworks in which bet-hedging is found do not define fitness as the ratio of reproductive values, but rather in terms of unweighted number of offspring. Thus, there is no mathematical disagreement here, and the issue of which kind of definition to use in what circumstances should be settled by how natural the biological interpretations are in the two cases. The generality and simplicity of the structure explained in the current paper is a strong argument in favour of thinking about evolution in terms of fitness defined following Fisher (1930), though the possible loss of the ecological significance of mean fitness, to be discussed in the next section, was not foreseen by Fisher.

The stationarity that comes with the stationary Markov environments was alluded to above, and it resolves the paradox that ‘in the long run we are all dead’ (to abuse horribly the famous sentence of Keynes, 1923, page 80). We are interested in how natural selection acts in a given environment, and we expect natural selection to improve an organism’s fit to its environment, but this is environment in a generalised sense. It does not mean the current environment this year, but the general pattern of environments, including their sequences and correlations. Thus, to study natural selection we need to specify that environment, that is, make enough assumptions about that generalised environment that we can ask whether natural selection is improving or not. In specifying the environment, we take a necessary step in understanding an organism’s fit to it. This assumption, rather than the reality of an infinitely distant generation, is enough to provide reproductive values. The question of how long the long term has to be can be asked of any study of natural selection, and the nature of random environments could make that a little longer, but

does not change the underlying logic.

This section shows that fitnesses and reproductive values are not brute facts about the world. Rather, they depend on assumptions that we make about the population and how it interacts now and will interact in the future. These are working assumptions, made because we have to, but also because the operation of natural selection depends on and is a response to the whole generalised environment. Rather than hide these assumptions by pretending fitnesses are brute facts, it is more useful to acknowledge the role of the working assumptions, which would even allow us to use and contrast different sets of working assumptions.

### 4.3 Total population reproductive value

Fisher (1927) produced a very famous demographic result, which was that if population size is measured by the total reproductive value, then the population is always growing at a constant exponential rate, and that rate is given by the Malthusian parameter. Our assumption that the reproductive value of a class equals the sum of its shares of the reproductive values of next year's classes implies that the total reproductive value of the population remains unchanged, and this is why we have the unfamiliar result that the mean fitness always equals one, whereas for Fisher, the mean fitness equalled the Malthusian parameter. What is at stake in this difference, and which option should be preferred?

Here, Fisher's own definitions are considered:

It has not to our knowledge been noted before that Fisher (1930)'s verbal and mathematical conceptions of reproductive value are inconsistent with each other. Fisher describes reproductive value on page 27 as answering the question "To what extent will persons of this age, on the average, contribute to the ancestry of future generations?". But the contribution to future ancestry of an individual must equal the sum of its genetic share of the contributions of its offspring, as the contribution is made up of those parts, whereas in Fisher's mathematical definition he discounts offspring contributions by the time of their production, using a discount factor that turns out to equal the population growth rate. Fisher never uses his concept to decide whether a 40 year old in 1930 makes the same contribution to 'the ancestry of future generations' as a 40 year old in 1958, but his two definitions would give different answers (except in populations with a zero growth rate). Crewe et al. (2018, page 1087)

Fisher was interested in a population that grew in size indefinitely, perhaps because he did not want to entertain the complications of density dependence,

perhaps because he was interested in human population growth which looked at the time as though it might well grow for some considerable time. In the framework of the current paper, there is no problem with a population that grows, but the per capita reproductive values do get smaller so that the total reproductive value remains constant.

Fisher’s discounting allows him to ensure that his reproductive values remained constant over time, so that a 40-year-old man would have the same reproductive value no matter what the size of the population, and adding up all the reproductive values would give one measure of population size. While this seems quite useful, the trick works only if the projection matrix remains unchanged over time (or a fixed cycle over time, see Bacaër and Abdurahman, 2008), and in Section 4.1 we saw that assumption did simplify models a lot, but was not biologically reasonable. Once the per-capita reproductive values may change, it is unclear if there is a way to give meaning to the total reproductive value – there is a ‘numéraire problem’ about how to choose the basic unit. It seems unlikely Fisher’s approach can be generalised, but there is a challenge for mathematical biologists to find that generalisation, or prove there is none.

Thus, Fisher’s approach is fine under the standard assumptions but cannot be maintained as a principle more widely, and this paper therefore prefers the constancy of total reproductive value. However, in one situation, Fisher’s approach is in fact useful, and it is important to mention it here. Biologists often assume a bland density dependence, in which the model shows an exponentially increasing population, but the biologist thinks ‘I will take the relative numbers of each age class seriously, but ignore the total population size. That allows me to keep the model and incorporate a crude form of density-dependence.’ Here, the discounting of reproductive value is indeed appropriate, but is properly understood rather differently. The more principled way to operate the same model is to take seriously the fixed population size, and to maintain it by imposing an additional density-dependent but age-independent rate of mortality. This model would give the same observable outcomes as the slight abuse of Fisher’s model: this works through the new reproductive values decreasing with age relative to the unprincipled values, in a way that exactly matches the discounting of the less-principled approach.

Thus, it would be a shame to lose the ecological aspect of fitness when considering structured populations, but perhaps the correct view is that the structure of the population and class interrelations are not the right place to look for an ecological measure. The forces of density-dependence provide a more logical source for an ecological measure of population size, as Lande et al. (2009, 2017) have found. There is challenge here for mathematical modellers, to find a way round my gloomy conclusion, by discovering a way to measure population size that maintains all the evolutionary properties of fitness, and simultaneously

the ecological property that mean fitness equals the population growth rate, with these properties holding both in and out of demographic equilibrium.

This section concludes by considering whether an unweighted Price Equation can be useful, in response to a referee’s suggestion. The Price Equation can be used for partitioning the change in a mean population quantity over time, and dividing it into a selection component and a property-change component, as Frank (1998, 2012) has emphasised. The rationale for weighting by reproductive value is to ensure that the selection component is zero whenever there is no selection going on (e.g. when there are no genetically-caused phenotypic differences currently expressed in the population). This property is necessary when discriminating selection from other forces is important. If the Price Equation is used for another purpose, perhaps as a convenient method of calculation, then the right weighing to use would reflect that other purpose, and this might sometimes be equal weights.

#### 4.4 An alternative definition of fitness

Here, we consider a different and incompatible definition of fitness to the one described above. The possibility of incompatible definitions that both claim descent from Fisher (1930) arises because of the remarkable fact that the term fitness, which occurs as ‘mean fitness’ on the left hand side of the fundamental theorem, and as ‘genetic variance of fitness’ on the right hand side, is not actually defined by Fisher anywhere in his book or, indeed, elsewhere.

A route taken by Kimura (1958) and followed by Crow (1979) and Lessard (1997) is to define fitness separately for each genotype, rather than for each individual. The origin of the suggestion is clear. Fisher does not explicitly define fitness, but it enters into two kinds of relationships with other variables: first, as above, as an individually-defined value as the ratio of the two kinds of reproductive values, and second, the mean of that first kind of fitness equals the Malthusian parameter. Kimura followed the second of Fisher’s approaches. He took the vital statistics i.e. the birth and death rates for each genotype, and found the Malthusian parameter of a hypothetical population all of whose members have those vital rates. Specifically, he found the value of  $m$  that solves the Euler-Lotka equation for vital rates  $(\mu_x, b_x)$ , the death and birth rates at age  $x$ , where  $l_x = \exp(-\int_0^x \mu_z dz)$  is the chance of surviving until age  $x$ . The equation is

$$\int_0^\infty e^{-mx} l_x b_x dx = 1,$$

and value of  $m$  for a genotype is then assigned as the fitness of all individuals with that genotype. The population is hypothetical if the genotype in question does not breed true. Lessard (1997) goes on to calculate reproductive values,

using Fisher’s formula with the genotype’s own Malthusian parameter and its own vital statistics (and making the arbitrary assumption that the reproductive value of newborns of all genotypes should equal one).

Kimura’s approach fails the test of neutrality for fitness definitions, as using this definition can show selection at work, when there are no genetically-caused phenotypic differences in the population, as the following example shows. Suppose an age-structured population has two different types, one of which has an increased survivorship from the age of eight onwards, but up to age seven both types have identical birth and death rates. Then suppose the population currently has only four year olds and younger: there should be no natural selection until some members of the population reach eight years old, as no gene frequency changes are due to genetically-caused phenotypic differences. This property is upheld by the fitness defined in the rest of this paper, but not by Kimura’s suggestion, as it calculates the growth rate of the population on the basis of demographic equilibrium of ages for the given genotype, which includes the eight year olds and above. Thus, the neutrality condition helps us choose between these very different definitions of fitness.

## 4.5 Mathematical literatures

There are many mathematical literatures dealing with natural selection. Here, some are connected to the current perspective. The most rigorous literature of mathematical population genetics is displayed in the textbooks of Ewens (1979, 2004). However, that strand is largely unconcerned with characterising natural selection. Indeed, despite exchanges about these questions, authors in that area do not really recognise the questions as worth pursuing (Ewens and Lessard, 2015; Lessard and Ewens, 2019). The major exception is the fully engaged work of Charlesworth (two decades of work with colleagues are brought together in Charlesworth, 1994), who brings the mathematical population genetic tradition to work on underlying fundamental principles of behavioural ecology, including inclusive fitness, fitness maximisation, and the theory of evolutionarily stable strategies. Charlesworth also puts together the class structures of sex and age, and resolves issues with the concept of demographic female dominance. Two literatures working closer to more recent biology centre on Taylor and coworkers (Taylor, 1990, 1996; Taylor et al., 2007) and Rousset and coworkers (Rousset, 2004; Lehmann et al., 2006), which both speak to the concerns of behavioural ecologists and concepts related to natural selection, including reproductive value. The latter literature has recently begun to engage in depth with the idea of individual fitness maximisation, as understood by behavioural ecologists, linking it to more traditional population genetics (Lehmann et al., 2015, 2016; Lehmann and Rousset, 2020).

## 5 Discussion

Fisher (1930)’s careful structure of reproductive values and fitness allowed the fundamental theorem to tell us how much natural selection was going on in a population, and what natural selection was improving, but was very poorly communicated, and biologists did not understand his concept of fitness at all until Price (1972b)’s exposition of the fundamental theorem. This paper sets out to explain clearly what Fisher’s concept of fitness was, and why it is useful.

Queller (2017) usefully identifies a number of mathematical results as fundamental to our understanding of evolution, and derives them all from the Price Equation. He somewhat dethrones Fisher’s result by sharing the title of ‘fundamental’. This paper suggests Fisher deserves credit for allowing class structure in his fundamental theorem, whereas the other results by other workers do not, at least as they expressed them. And once we admit classes, even to the extent of age structure, it is the original fundamental theorem that confirms the success of representing Darwin (1859)’s central insight that natural selection is an improving process, through Fisher’s joint identification of a definition of fitness, on the one hand, and of a method of separating out the effect of natural selection, on the other.

A second minor quibble follows with Queller’s excellent analysis. He is happy to accept that the results he discusses are approximate, as a tradeoff for their generality and simplicity. All results, regarded as aiming to match reality, are approximate, of course. But technically, the fundamental theorem, given its assumptions, is not an approximation if, following Price (1972b), the left hand side of the fundamental theorem is written as the partial change in mean fitness, in particular that part due to natural selection.

Figure 1 of Queller (2017) very usefully displays a variety of mathematical results that help biologists think about evolution and natural selection. The current paper argues that these results can all be extended very straightforwardly, using the equation of Price (1972a) and its generalisation by Crewe et al. (2018), to allow class structure and environmental uncertainty, by adopting the structure of basic reproductive value, Williams’s reproductive value, and fitness, as derived from Fisher’s original fundamental theorem. Fisher’s concept of fitness, therefore, has an important role to play in biologists’ thinking about natural selection.

## 6 Acknowledgments

I am very grateful to Prof. Sébastien Lion and an anonymous referee for very helpful comments.

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