Mathematical Biology

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A theory of Fisher's reproductive value

Abstract. The formal Darwinism project aims to provide a mathematically rigorous basis
for optimisation thinking in relation to natural selection. This paper deals with the situation in
which individuals in a population belong to classes, such as sexes, or size and/or age classes.
Fisher introduced the concept of reproductive value into biology to help analyse evolutionary
processes of populations divided into classes. Here a rigorously defined and very general
structure justifies, and shows the unity of concept behind, Fisher's uses of reproductive value
as measuring the significance for evolutionary processes of (i) an individual and (ii) a class;
(iii) recursively, as calculable for a parent as a sum of its shares in the reproductive values of
its offspring; and (iv) as an evolutionary maximand under natural selection. The maximand is
the same for all parental classes, and is a weighted sum of offspring numbers, which implies
that a tradeoff in one aspect of the phenotype can legitimately be studied separately from
other aspects. The Price equation, measure theory, Markov theory and positive operators
contribute to the framework, which is then applied to a number of examples, including a
new and fully rigorous version of Fisher's sex ratio argument. Classes may be discrete (e.g.
sex), continuous (e.g. weight at fledging) or multidimensional with discrete and continuous
components (e.g. sex *and* weight at fledging *and* adult tarsus length).

Contents

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1. Introduction

The concept of reproductive value was introduced into biology by Fisher (1930), and is now used in the study of age-structured populations (Charlesworth, 1994) and by ecologists in the study of populations with age and other kinds of structure too (Caswell, 1989; Easterling et al. , 2000). Reproductive value is a quantitative measure for subsets of a population, including individuals, that indicates their relative importance in evolutionary processes. In fact this paper will show that the quantitative measure plays four roles. Some are more familiar to biologists, others to population geneticists, and the analysis will show that the roles are all tightly interlinked.

First, each individual in the population has a numerical value attached to it that is its reproductive value, and when taking an average gene frequency, the reproductive values should be used as individual weights. The sense of 'should' is that if we do so, average gene frequency will behave nicely. For example, if there are two alleles at a locus and they have identical effects, their average gene frequencies won't change. Thus an individual's reproductive value measures its contribution to the gene pool of future generations.

Second, subsets of the population, such as males and females, or large and small, have reproductive values, and when calculating an average gene frequency over the whole population, they should be used as weights: note that the reproductive value of a subset, apart from some possible re-scaling for convenience, does equal the aggregate of the reproductive values of the individuals in the subset. One interest here is that sometimes it is possible to calculate the reproductive value of a whole subset, knowing nothing about the individuals, as in Fisher's famous sex ratio argument showing that in diploids all males together have the same reproductive value as all females together. In this sense, we can think of the reproductive value of all males as the fraction of genes in a future generation whose ancestor is present in a male in this generation. Hence the reproductive value of a subset measures its genetic contribution to future generations.

Third, an offspring has a reproductive value, and each parent has a share in it, depending on the fraction of the offspring's genes it contributed; the reproductive value of a parent equals the sum of its shares in the reproductive value of its offspring. This reveals reproductive value as a generalisation of counting a parent's offspring, and it also becomes possible to ask what the parent's reproductive value would have been if different strategies had been followed.

Finally, there is a role as maximand. In simple models without classes, a gene frequency increases if the gene confers higher number of offspring on its bearers. This can be translated into more formal links showing that natural selection

tends to lead to maximisation of number of offspring or, more precisely, of expected relative number of offspring (Grafen, 2002). By using reproductive value as weights, we will obtain a generalisation to the case with classes: average gene frequency (when weighted with reproductive value) increases if the gene confers a higher reproductive value on its bearers. This gives us a maximisation principle for reproductive value, though it will not made formally explicit until the examples in Section 8.

It is worth noting that there has been confusion in discussing 'evolutionary maximands' between dynamic concepts such as Lyapunov functions and potential functions on the one hand, and on the other, the idea that individual organisms will be selected to act as if maximising some function. It is the second that will be discussed here, and the reader is referred to Grafen (1999) for further discussion.

There are many significances in establishing such a reproductive value in a wide range of models. At the most obvious level, it helps to tame complex situations with classes, and provides results parallel to the simple model with only one class. More ambitiously, it brings precision to the biologist's frequent use of 'reproductive value' as a more precise version of 'fitness'. It leads mathematical population geneticists to see that the first three properties, with which they are familiar in particular contexts, hold very generally and are linked to maximisation. It extends the range of models in which an optimisation principle has already been demonstrated (Grafen, 2002, 2006) to include models in which classes exist. Population geneticists have since an influential paper of Moran (1964) rejected the concept of an optimisation principle in population genetics, so it is relevant that this paper establishes the nature and existence of reproductive value in a very general setting with full mathematical rigour. Finally, the paper shows that the original informal use of reproductive value (Fisher, 1930) can be fully justified in that very general setting.

When, from a biological point of view, does the concept of reproductive value of classes become important in applications? Examples include sex ratio, where offspring may be male or female; parental care, in which offspring receiving more care must somehow count more than those who receive less; and geography, where the location of an offspring may matter. A technical example is age-structured populations, which can be handled within a non-overlapping generations framework by treating survival from year t to year $t + 1$ as the production by an age t adult of an asexual age $t + 1$ offspring. It is also possible, for example, to define classes in the population with respect to one genetic locus while studying changes in gene frequencies at another.

The current paper builds on the work of Taylor (1990, 1996), who considered a finite set of classes. Here the analysis is linked explicitly to Fisher's reproductive value arguments, showing that Fisher used a very general framework we are only now coming to understand. By allowing the set of classes to be finite or infinite, and to include single and multi-dimensional continuous variables, the range is extended of examples to which reproductive value can be applied. Finally, the treatment here contributes to the formal Darwinism project (Grafen, 1999, 2000, 2002, 2006), which aims to represent in as general a way as possible Darwin's arguments about the operation of natural selection. The arbitrariness of the set of classes, and the

fact that the argument handles them all in a single formulation rather than providing separate cases for different kinds of sets, contributes significantly to the claim that the project captures Darwinian natural selection in general. It is also important for the project that some of the results obtained here apply under a more general genetics than Taylor's.

The formalism developed in this paper therefore allows new kinds of examples to be studied using reproductive value methods. One so far hypothetical example would be of parental care in birds, where the type of care provided by parents affects the fledging weight and tarsus length of sons and daughters. The reproductive value weights would provide a maximand that would allow a parent to choose which combination of fledging weight and tarsus length was best for sons, and which was best for daughters. The optimal balances could be different for parents from different classes. Suppose tarsus length is used in mate choice. The weights would then incorporate sex-ratio selection and sexual selection, as well as any differences in simple viability, to provide a single quantity with important properties under natural selection that biologists might well be tempted to call 'fitness'.

There are important restrictions on the analysis. To incorporate classes in the absence of uncertainty, it has proved necessary to assume the population is infinite. We also assume discrete, non-overlapping generations and that an individual remains in the same class throughout its life, which excludes important areas of reproductive value. For example, reproductive value has been used to study sex ratio under partial bivoltinism (Grafen, 1986), and to study cases in which individuals can affect their own class from one year to the next (Grafen, 1987). Thus, we deal here only with classes that are chosen by parents, and that offspring bear for their lifetime. Defining reproductive value outside these assumptions is an important task.

There are further restrictions. Individuals are assumed to affect only their own number of offspring, so that social behaviour as introduced by Hamilton (1964) is excluded. Grafen (2006) incorporates social behaviour into the formal Darwinism project, but not in a way that combines it with classes and reproductive value. Frequency-dependent selection is not explicitly modelled, and most forms of it would require a more elaborate model, and a more complex analysis, than that presented here. However, sex ratio selection is included.

Some sections are designed to be readable by non-mathematical biologists, who are prepared to endure some necessary limited notation. Section 2 provides an overview of the rest of the paper without mathematical technicalities, and then an account of the mathematical manoeuvres employed in each section. Section 5 gives a reasonably non-technical explanation of how the concept of reproductive value links to the formal idea of invariant measures, and of the biological significance of non-uniqueness. Section 7 discusses Fisher's uses of reproductive value, and how the analysis of the current paper justifies the implicit structure, while Section 10 briefly concludes. The other sections are quite technical, and require some mathematical ambition.

2. Overviews of the paper

A marked feature of this paper is that the mathematics presented is very formal, and daunting even to the author. This overview section first presents an outline of the paper, section by section, without technicalities. The following subsection discusses the mathematical concepts used, explains the need for the formalities, and justifies the absence of a simple pedagogical example.

2.1. An overview in words

The main purpose is to provide a mathematically rigorous exposition of how optimisation ideas can be applied to the operation of natural selection when the population is divided into classes. There are a number of steps. First, Section 3 derives the Price Equation in the presence of classes, and then focusses on how genes flow from class to class across the generations. The pattern of flow is used to define the reproductive values of the classes. Section 4 considers whether a pattern of flow always defines reproductive values, and if so, whether it defines them uniquely. It also establishes the central property that reproductive value allows an evaluation in one generation of the asymptotic number of descendants. This is a highly technical section, but the biological interpretation of these issues is set out as intelligibly as possible in Section 5. Although no fully general result can be established, it is likely that reproductive value can be defined in a wide range of biologically useful situations.

The target of selection, which becomes the maximand individuals are selected to act as if maximising, has two important features. It is the same for parents in all classes. It is a sum of contributions to offspring, weighted by offspring class, and so tradeoffs in one aspect of phenotype can legitimately be separated from other aspects.

Section 6 studies equilibrium concepts of gene dynamics, an essential part of studying the operation of natural selection. The 'tracer-allele' approach (Seger & Stubblefield, 2002) is adopted, but there is an ambivalence of concepts that requires some discussion. The first main result is one of the defining properties of reproductive value identified by Fisher (1930) and later authors, that it allows a way to measure natural selection that has the following desirable property: no matter how two alleles are distributed across classes, there is no net selection if their phenotypic effects are identical. If we use any other weights to aggregate the gene frequency changes across classes, then two alleles with identical effects can undergo selective change relative to each other. The second result shows how reproductive value provides a maximand for an optimisation approach to the outcome of natural selection.

Section 7 reviews the uses of 'reproductive value' by Fisher (1930), and shows how they can be formally justified in detail. This section therefore shows that the elaborate mathematical machinery constructed in earlier sections has considerable biological significance. In particular, it shows that reproductive value provides a maximand of natural selection, in the sense that natural selection tends to lead to individuals who act as if maximising their reproductive value.

The mathematical machinery of earlier sections is put to use in Section 8, in three examples that are only a sample of the range of possible applications, but

which do show how the very abstract formulations can be brought to bear on particular cases. A fully rigorous version of Fisher's sex ratio argument is given, along with a development only possible using the results of this paper. Then there is an example of parental care where the classes belong to an interval on the real line, and a geographical example where class represents location. These examples are all small-scale, as a substantial example would require a paper of its own.

In Section 9 the links with the work of Taylor (1990, 1996) are discussed. There is a small concluding section.

2.2. A mathematical overview

The considerable mathematical machinery is all needed for a purpose. Here, some of the choices are explained. Section 3 introduces a model beginning with the set of individuals I, which is assumed infinite. The set of classes X is treated in a very general way: technically it is assumed to be compact Hausdorff. This means X is a compact topological space, and for every ordered pair of distinct points there is an open set that contains the first of the pair but not the second. X is thus permitted to be any compact subset of $\mathbb{R}^n$, which seems general enough for many biological purposes. Infinite-dimensional phenotype spaces have been used (e.g. Grafen, 1990), and so the capacity to handle infinite-dimensional spaces of classes may also be useful – though note that the space must be compact. Both I and X are treated as measure spaces, and the distribution of offspring classes produced by each individual is treated as a measure over X. The frequency of alleles is studied using the covariance selection mathematics of Price (1970), but not the later extensions of Price (1972). The machinery of measure theory is required because of the desire to present a single argument covering all cases: the simpler notation for finite X or for densities on the real line would not have covered the other of those cases. The population I is assumed infinite to allow exact results to be obtained. A finite I over an infinite X could only adopt an atomic distribution; and finite I would not ensure that fairness of meiosis on average guaranteed fairness of meiosis in outcome. Another important reason for using measure theory is that the set of densities does not form a complete space and existence results would fail: a sequence of densities can converge to a distribution with atoms. It is quite likely in applications that equilibrium distributions would have atoms, and also that optimal responses would be atomic distributions.

Once it is decided to use measure theory, it becomes difficult to follow the very reasonable suggestion of referees of an earlier version, to provide a simple mathematical example to explain the concepts. The added notation required, and the different kind of notation required for discrete X or to consider densities on the real line, would render unwieldy the already considerable mathematical notation of the paper. Many of the concepts are developed for discrete X, and explained very well, by Taylor (1990, 1996), who could be read alongside.

The use of Radon-Nikodym derivatives should be mentioned. If we have a measure over a space, and an L^1 function on that space, it is a standard result that we can produce a new measure by integrating the function with respect to the original measure. The inverse process, of finding the L^1 function that will convert one measure

into another, is Radon-Nikodym differentiation, and it will be needed in various contexts because I and X are measure spaces.

Another formalism introduced in Section 3 is a Markov process over the state space X. The Price Equation takes us from parents in one generation to offspring in the next. Markov theory is used to extrapolate the effects on gene frequencies that would follow if the class-to-class transition pattern from one generation to the next were to be repeated indefinitely. This hypothetical repetition allows reproductive value to be defined in terms of an invariant measure of the Markov process.

The questions of existence and uniqueness of that invariant measure are the subject of Section 4. The general applicability of the concept of reproductive value depends on how widely an invariant measure exists for the Markov process of the preceding section. Theorems are drawn from the literature and are applied in general, and in a series of examples that also shows how the mechanics of the Markov process work. Although an example is found in which none of the general results guarantee existence, even there an invariant measure is exhibited: the general sense is that reproductive value exists in most biologically plausible cases with a stable distribution of the population over classes. The section actually begins by defining a 'forwards process', which follows gene frequencies forwards in time: this corresponds to the 'backwards process' represented by the Markov process, which follows reproductive value backwards in time. The forwards process is useful in studying the backwards process, and also in considering equilibrium concepts later in the paper. The invariant measure is by no means always unique, and the nature of sets of invariant measures is discussed along with their biological significance in Section 5.

Section 6 looks at equilibrium under natural selection, finding a very natural result linking equilibrium in the presence of classes to conditional expectations. Optimisation results can be obtained very generally in Darwinian models (Grafen, 2002, 2006). One of the main purposes of the project is to set the strategic approach on an equal footing with the population genetics approach in terms of mathematical rigour, so that choices between them can be made on the grounds of biological utility. It is therefore significant, and requires discussion in Section 6, that when classes are added, there is an ambivalence of equilibrium concept even within the strategic approach.

Explicit optimisation programs are employed in the examples in Section 8, where it is easier to do because the need for complete consistency and generality no longer holds. In previous papers (Grafen 2002, 2006) explicit optimisation was employed in general, as there was substantial work to do at that level, for example incorporating uncertainty into the maximand of natural selection. In the current paper, the additional notational requirements would not have been worthwhile.

Section 9 includes the correspondents in this paper to the left and right eigenvector results for the forwards and backwards processes of Taylor (1990, 1996).

3. Price for classes

This section aims to develop the covariance selection mathematics of Price (1970) as applied to a population whose members and whose members' offspring each

belong to a class. The approach chosen employs measure theory rather than the alternative of generalised functions (Kanwal, 1983), for compatibility with previous work extending the Price equation to uncertainty (Grafen, 2002). This holds out the prospect of a combined model developing a rigorous treatment of the case combining classes and uncertainty.

The Price equation assumes a census point in the parent and offspring generations. All individuals at the first census point are parents, and each leaves a certain number of successful gametes, that is, gametes which contribute to an offspring present at the second census point. We will assume in the words we use that the contribution of a parent to an offspring is exactly one gamete, which holds for most situations in diploidy, haploidy and haplo-diploidy. The formalism actually extends more widely, if we understand counting offspring to be counting successful gametes. This extension matters because the framework does apply to a model of mixed sexual and asexual reproduction in diploids, for example, including where parental survival is formally represented as asexual reproduction; and to the arbitrary ploidy models of Grafen (1986), as in Section 8.1. However, it would be too cumbersome to have to read 'successful gamete' in all the necessary places. We immediately assume, though it is not needed until Section 4.1, that all individuals in the same class share the same ploidy.

Let the set of parent individuals be represented by a measure space $(I, \Im, \mu_I)$, where the measure μ_I weights individuals by their ploidy. Let the set of classes be represented by a compact Hausdorff space X. This allows X to be, for example, an arbitrary compact subset of $\mathbb{R}^n$. Equipped with its σ-algebra of Borel subsets $\mathfrak{X}$, $(X, \mathfrak{X})$ is a measurable space. Let there be a measurable function $\chi : I \to X$ denoting the class of a parent.

In order to operate with measures, we introduce $\mathcal{M}(X)$, the space of signed finite measures over X. This is a Banach space (see e.g. Schechter, 1997, 29.29g, page 803), and so we may integrate and take expectations of measures (Schechter, 1997, 23.16, page 615). $\mathcal{M}(X)$ is a measurable space in combination with its Borel sets derived from the usual topology. We assume that offspring are produced according to a measurable function $w : I \to \mathcal{M}(X)$. $w(i)$ is a non-negative measure belonging to $\mathcal{M}(X)$, and represents the measure over offspring classes produced by parent i. It will be convenient to assume that the total production of offspring by individuals is uniformly bounded, formally $w(i)(X) \le w_{max}$. We define the total offspring production by class, $W \in \mathcal{M}(X)$, and implicitly the expectation $\mathbb{E}[\cdot]$ over the measure space $(I, \Im, \mu_I)$, by

$$W = \int_I w(i)\mu_I(di) = \mathbb{E}[w] \tag{1}$$

Following Grafen (2000), we introduce a p-score, a measurable function $p : I \to \mathbb{R}$, to represent an allele frequency, or weighted sum of allele frequencies, in individuals $i \in I$. The p-score for an individual is thus the mean of the p-scores of the gametes that contribute to its genome. The mean p-score by class among parents is given in I by the conditional expectation $\mathbb{E}[p \mid \chi]$: conditioning on a measurable function will be used throughout as a shorthand for conditioning on the sub-σ-algebra defined by the level sets of that function. Letting $\mu_X \in \mathcal{M}(X)$ be defined as the

measure of parent classes over X, formally $\mu_X(A) = \mu_I\{i : \chi(i) \in A\}$, we shall let π be a μ_X-measurable function from X to $\mathbb{R}$, also representing the mean p-score among parents by class, defined by the function composition $\pi \circ \chi = \mathbb{E}[p \mid \chi]$. (The reader is reminded that a conditional expectation is a member of the same L^1 as the function whose expectation is taken, in this case of $L^1(\mu_I, \mathbb{R})$.)

The extension from allele frequency to p-score is possible because both the left and right hand side of the Price equation are linear in allele frequency, so any weighted sum of allele frequencies also obeys the Price equation. Because allele frequency is measured as a proportion of the individual's ploidy, there is no automatic tendency for individuals with a higher ploidy to have a higher p-score.

The mean p-score among offspring will be denoted $\pi' \in L^1(\mu_X, \mathbb{R})$, and we proceed to find a formula for it. Informally, the contribution of individual i to the offspring at x is $w(i)(dx)$, and because we have assumed perfect transmission and an infinite population, the p-score contributed by individual i may be taken as $p(i)$. We will use more general notation, and suppose that some property $f(i)$ is passed on to the offspring. Thus we could hope to write the average value of f among the parents of offspring at x as the weighted average

$$\frac{\int_{i \in I} f(i)w(i)(dx)\mu_I(di)}{\int_{i \in I} w(i)(dx)\mu_I(di)} \tag{2}$$

If we move the dx outside the integral sign we obtain

$$\frac{\left(\int_{i \in I} f(i)w(i)\mu_I(di)\right)(dx)}{\left(\int_{i \in I} w(i)\mu_I(di)\right)(dx)} = \frac{\mathbb{E}[fw](dx)}{\mathbb{E}[w](dx)} = \frac{\mathbb{E}[fw](dx)}{W(dx)} \tag{3}$$

Now this last expression is in fact well-defined. The classic Radon-Nikodym theorem (Schechter, 1997, 29.10, page 790; 29.20, page 796) applies to two real-valued measures over the same arbitrary measure space, on condition that the numerator measure (which may be signed) is absolutely continuous with respect to the denominator (which must be positive and finite). In this case we need to establish that $\mathbb{E}[w](A) = 0$ implies $\mathbb{E}[fw](A) = 0$, for all $A \in \mathfrak{X}$. If $\mathbb{E}[w](A) = 0$, then as $w(i)$ is non-negative, it follows that $w(i)(A) = 0$ for almost all i. So $f(i)w(i)(A) = 0$ for almost all i and $\mathbb{E}[fw](A) = 0$ as required. The conclusion of the theorem is that there exists a function $k \in L^1(W, \mathbb{R})$ defined W-almost everywhere such that for every measurable A,

$$\int_A k(x)W(dx) = \left(\int f(i)w(i)\mu_I(di)\right)(A) \tag{4}$$

This formula shows that despite the informality of equation (3), we can define a function $k(x)$ that gives the average value of f among the parents of offspring at x.

It will be convenient to represent a Radon-Nikodym derivative with respect to W as $\mathbb{D}_W$. Our first application of Radon-Nikodym derivatives is to define π', W-almost everywhere, by

$$\pi' = \mathbb{D}_W \mathbb{E}[pw] \tag{5}$$

Now employing linearity of expectations and the identity $p = \mathbb{E}[p \mid \chi] + (p - \mathbb{E}[p \mid \chi])$ yields

$$\mathbb{E}[pw] = \mathbb{E}\left[\mathbb{E}[p \mid \chi]w\right] + \mathbb{E}\left[\left(p - \mathbb{E}[p \mid \chi]\right)w\right] \tag{6}$$

and the next stage is to link the argument so far to the theory of Markov processes.

3.1. Link to Markov theory

The Price Equation has linked genotype frequencies and reproductive output in one generation to gene frequency change between that and the subsequent generation. If each different class continued to produce the same distribution of classes among its offspring over many generations, there would be important consequences for gene flow through the classes. To work with these consequences, we introduce Markov theory, and do this in a very formal way because precise theorems will be applied in due course.

Rosenblatt (1971, Chapter IV, section 2) deals with a probability transition function $P \colon Z \times \mathfrak{Z} \to \mathbb{R}$ on a compact Hausdorff space Z equipped with its Borel sets $\mathfrak{Z}$ and a measure ν. $P(x, A)$ represents the probability that state x will be succeeded by a state in the subset A of Z. Associated with the process defined by P is a linear operator $T \colon L^1(\nu, \mathbb{R}) \to L^1(\nu, \mathbb{R})$. The linear operator T is defined by $(Tf)(x) = \int P(x, dy)f(y)$, and if $f \in L^1(\nu, \mathbb{R})$ represents some function over Z, then (Tf) is another function over Z, with $(Tf)(x)$ representing the average value of f over the successor states of x. $(T^j f)(x)$ represents the average of f over the successor states of x after j transitions. If it happens that T takes continuous functions to continuous functions, then $P(x, A)$ is not only a measure on $(Z, \mathfrak{Z})$ for almost all x, but also a measurable function of x for fixed A.

The connection we make between the biology and the Markov theory reverses the direction of time. We will understand $P(x, A)$ to represent the probability that a random allele of a random individual in class x derives from a parent in a class in the subset A of X. $(Tf)(x)$ represents the average of f over the parents of individuals in class x. We note that this reversal introduces into the calculation of P the requirement to know the distribution of the population over classes. Thus, the reversed version lacks the straightforward nature of the original interpretation in which the mechanics of the Markovian process determine $P(x, A)$, and the distribution over states can be derived from it.

The Markov process is to be defined over X, and the associated measure we will take to be W, the distribution of offspring. Then the equations that link the Price equation development with Rosenblatt's notation are as follows:

$$P(x, A) = \left(\mathbb{D}_W \int_{i \colon \chi(i) \in A} w(i)\mu_I(di) \right)(x) \tag{7}$$

$$(Tf) = \mathbb{D}_W \mathbb{E}\left[(f \circ \chi)w\right] \tag{8}$$

These equations define a Markov process over X, provided the definition of T does take $L^1(W, \mathbb{R})$ into itself. To ensure this later, we will need to assume that μ_X, the

parental distribution over states given by $\mu_X(A) = \mu_I\{i : \chi(i) \in A\}$, is absolutely continuous with respect to W. The biological interpretation of this condition is that any subset of states that includes parents must also include offspring: a population may thus be expanding into new classes, but not abandoning any occupied classes. This is so that the Markov process can be extrapolated backwards in time on the basis of the gene flow pattern in this generation.

If we let f_A be the indicator function of A and then define the finite measure $u_A = \int_{i:\,\chi(i)\in A} w(i)d\mu_I(i)$, we can also write P as

$$P(x, A) = (Tf_A)(x) = \frac{u_A(dx)}{W(dx)} = \frac{du_A}{dW}(x) \tag{9}$$

Invariant measures for T play a central role in the development of the theory, defining reproductive value itself for reasons explained verbally in Section 5, and we now introduce relevant notation and concepts. Let $\mathcal{M}_\sigma(X)$ denote the subspace of $\mathcal{M}(X)$ containing the measures that are absolutely continuous with respect to $\sigma \in \mathcal{M}(X)$. Let the operator $\mathbb{I}_\sigma$ represent the integral of f with respect to a measure $\sigma \in \mathcal{M}_W(X)$, as $\mathbb{I}_\sigma f$.

A measure $\tau \in \mathcal{M}_W(X)$ is said to be invariant for T if it possesses the following property holding for all $f \in L^1(W, \mathbb{R})$,

$$\mathbb{I}_\tau f = \mathbb{I}_\tau(Tf) \tag{10}$$

The restriction to measures absolutely continuous with respect to W is required, for otherwise the integral is not defined for all $f \in L^1(W, \mathbb{R})$. An invariant measure must therefore by definition possess this property, and so we note here that existence of an invariant measure implies that $\mathbb{D}_W \tau$ is well-defined.

We shall assume for the moment that an invariant measure exists, and work with an arbitrary choice if there is more than one. Section 4 discusses questions of existence and uniqueness. We will see that often $\tau(A)$ represents the reproductive value of a subset A of classes. A full biological interpretation of τ is given in Section 5.

3.2. The Price equation with classes

Returning to the mathematical development, these definitions first allow us to take the Radon-Nikodym derivative of equation (6), and use equation (5) to write

$$\pi' = (T\pi) + \mathbb{D}_W \, \mathbb{E}\left[\left(p - \mathbb{E}\left[p \mid \chi\right]\right)w\right] \tag{11}$$

The invariant measure allows us to define a scalar average p-score $\mathbb{I}_\tau \pi$. We integrate over equation (11) with respect to $\tau(dy)$, and then subtract $\mathbb{I}_\tau \pi$ from both sides. These integrations are permitted because by definition τ is absolutely continuous with respect to W. Because τ is invariant, $\mathbb{I}_\tau T\pi = \mathbb{I}_\tau \pi$ and so we have

$$\mathbb{I}_\tau(\pi' - \pi) = \mathbb{I}_\tau \mathbb{D}_W \, \mathbb{E}\left[\left(p - \mathbb{E}\left[p \mid \chi\right]\right)w\right] \tag{12}$$

Aiming to move the operators inside the expectation, we rewrite the right hand side as a double integral

$$\int \left(\mathbb{D}_W \int \big(p(i) - \pi(\chi(i))\big) w(i) \mu_I(di) \right)(x) \tau(dx) \tag{13}$$

Letting $h = \mathbb{D}_W \tau$, and using the change of variables formula for Radon-Nikodym derivatives (Schechter, 1997, section 29.13, page 791), we further obtain

$$\int h(x) \left(\int \big(p(i) - \pi(\chi(i))\big) w(i) \mu_I(di) \right)(dx) \tag{14}$$

It is now time for a fundamental operation that works out what the class distribution of the parents in the next generation will be. Begin by constructing a measure ν on the product space $I \times X$, with the product topology and product σ-algebra, defined by the distribution of parent-offspring pairs, given for rectangular sets $A \times B$ by

$$\nu(A \times B) = \left(\int_A w(i) \mu_I(di) \right)(B) \tag{15}$$

Absolute continuity is automatically satisfied, so we may apply the Radon-Nikodym theorem to construct a derivative of ν with respect to the product measure $\mu_I \times W$, namely a function $k \in L^1(\mu_I \times W, \mathbb{R})$ such that

$$\nu(A \times B) = \int_{i \in A, x \in B} k(i, x)(\mu_I \times W)(di \times dx) \tag{16}$$

Note that $k(i, x) \in L^\infty(\mu_I \times W, \mathbb{R})$, as we assumed $w(i)(X) \le w_{max}$. Then formula (14) can be rewritten as

$$\int h(x)\big(p(i) - \pi(\chi(i))\big)\nu(di \times dx) \tag{17}$$

$$= \iint h(x)\big(p(i) - \pi(\chi(i))\big)k(i, x)\mu_I(di)W(dx) \tag{18}$$

It is permitted to change the order of integration as the integrand belongs to $L^1(\mu_I \times W, \mathbb{R})$, and so obtain

$$\int \big(p(i) - \pi(\chi(i))\big) \left(\int h(x)k(i, x)W(dx) \right) \mu_I(di) \tag{19}$$

The inner integral belongs to $L^1(\mu_I, \mathbb{R})$ by Fubini's theorem, and so we may define the operator $\mathbb{F}_W^\tau : L^1(\mu_I, \mathcal{M}_W(X)) \to L^1(\mu_I, \mathbb{R})$ by

$$\mathbb{F}_W^\tau : w \to \int h(x)k(\cdot, x)W(dx) \tag{20}$$

Using this 'fitness operator', and translating back to expectations from integrals, we recall equation (12) and rewrite equation (19) as

$$\mathbb{I}_\tau (\pi' - \pi) = \mathbb{E}\left[\left(p - \mathbb{E}[p \mid \chi]\right)\mathbb{F}_W^\tau w\right]$$

$$= \mathbb{E}\left[p\left(\mathbb{F}_W^\tau w - \mathbb{E}\left[\mathbb{F}_W^\tau w \mid \chi\right]\right)\right] \tag{21}$$

where the second equality follows easily from standard results, for example Theorem 5.5.11 of Ash & Doleans-Dade (2000). Covariance forms immediately follow, using the definition of conditional covariance for some measurable function g, $\mathbb{C}[a, b \mid g] = \mathbb{E}[ab \mid g] - \mathbb{E}[a \mid g]\mathbb{E}[b \mid g]$,

$$\mathbb{I}_\tau (\pi' - \pi) = \mathbb{E}\left[\mathbb{C}\left[p, \mathbb{F}_W^\tau w \mid \chi\right]\right] \tag{22}$$

$$\mathbb{I}_\tau (\pi' - \pi) = \mathbb{C}\left[p - \mathbb{E}[p \mid \chi], \mathbb{F}_W^\tau w\right] \tag{23}$$

The covariances are defined and so finite because we assumed that $w(i)(X)$ is bounded.

The covariance equations (22) and (23) express the generalisation of the Price equation to include classes. For simplicity let us agree for this paragraph to use the term 'fitness' to refer to an individual's sum of its contributions to offspring weighted by reproductive value, namely $(\mathbb{F}_W^\tau w)(i)$. An appropriately weighted average change in p-score across classes, on the left hand side, equals the average over parental classes of the covariance between p-score and fitness; or, alternatively, equals the covariance over all adults between the deviation of their p-score from the average of their class, and fitness. These are the fundamental Price equations in a population with classes.

4. Existence and uniqueness of reproductive value

This section makes the promised return to questions of the existence and uniqueness of an invariant measure of the operator T, but first we study the 'forwards' process, to find another angle on obtaining reproductive value. The relationship between the two routes will be discussed, and existence and uniqueness will be considered in relation to both processes.

4.1. The forwards process

The forwards process describes the population measure of classes next generation as a function of the population measure this generation, on the assumption there is a single phenotype in the population. The building block is a function $v \colon X \to \mathcal{M}(X)$, a measurable function that tells us the offspring distribution produced by an individual in class x. We make the biologically reasonable assumption that v is uniformly bounded. Define an operator $\tilde{U} \colon \mathcal{M}(X) \to \mathcal{M}(X)$ by

$$\tilde{U}m = \int v(x)m(dx) \tag{24}$$

This section relies for standard functional analysis results on Vilenkin *et al.* (1972). $\tilde{U}$ is a positive operator, as $v(x)$ is a non-negative finite measure for each x; and it is continuous under the norm topology as v is bounded. The population distribution n generations after m is $\tilde{U}^n m$. An equilibrium of the class dynamics would be represented by a non-zero measure m such that $\lambda m = \tilde{U} m$ and $\lambda = ||\tilde{U}||$.

Associated with $\tilde{U}$ is its adjoint operator $\tilde{T}$ on a Banach space $BM(X)$ comprising the bounded measurable real functionals on X, under the supremum norm. $\tilde{T}$ defined by the formula

$$(\tilde{T} f)(x) = \int f(y)v(x)(dy) \tag{25}$$

is continuous as v is bounded. Of primary interest here is the possibility that there may be a non-negative leading eigenfunction h such that

$$\tilde{T}h = \lambda h, \text{ or } \int h(y)v(x)(dy) = \lambda h(x) \tag{26}$$

We will see that such a function will often justify the term 'per-capita reproductive value'. Further restrictions on v may allow us to identify narrower cones within $BM(X)$ than the non-negative functions within which an eigenfunction must lie.

As $\tilde{T}$ and $\tilde{U}$ are adjoint operators, it follows that $(\tilde{T}^r f, m)$ equals $(f, \tilde{U}^r m)$ for arbitrary f and m, using the parentheses to represent integrating the function with respect to the measure. From this flows the central property that

$$\frac{\int h(x)m_2(dx)}{\int h(x)m_1(dx)} = \frac{\int h(x)(\tilde{U}^r m_2)(dx)}{\int h(x)(\tilde{U}^r m_1)(dx)} \quad \text{for } r = 1, 2, 3 \ldots \tag{27}$$

The interpretation is that provided we agree to evaluate the number of descendants by a leading eigenfunction of $\tilde{T}$, to be called h, we can obtain a comparison between the asymptotic numbers of descendants of two measures of offspring m_1 and m_2 by simply integrating them with respect to h. The 'work' of computing through the generations is done by the eigenfunction.

If $\tilde{U}$ is to represent the evolution of a population with phenotype v this carries the implication that within a class, the reproduction of individuals is proportional to their ploidy. The only plausible biological version is that all individuals in the same class share the same ploidy, as assumed in Section 3.

4.2. *Links between the forward and backwards processes*

The main purpose of introducing the forward process is to allow a sharper definition of per-capita reproductive value as the eigenfunction of $\tilde{T}$. The backwards process defines it only W-almost everywhere, so that it is not defined in regions with no offspring, and even where there are offspring it is defined only up to W-equivalence. First we show how the definitions of the processes are linked. Note that the operators $\tilde{U}$ and $\tilde{T}$ associated with the forwards process have tildes to distinguish them from the operator T of the backwards process.

As a preliminary, we prepare to define the backwards process using X instead of I. Suppose there is only one phenotype present in the population, with reproduction described for all classes by $v : X \to \mathcal{M}(X)$, and let μ_X denote the measure of parents over X and V be the measure of offspring. Then the following equations link the processes over I and those over X:

$$v \circ \chi = \mathbb{E}\left[w \mid \chi\right] \quad \text{as members of } L^1(\mu_I, \mathcal{M}(X)) \tag{28}$$

$$\mu_X(A) = \mu_I(\{i : \chi(i) \in A\}) \tag{29}$$

$$V = \mathbb{E}\left[v\right] \tag{30}$$

where the expectation over the measure space $(X, \mathfrak{X}, \mu_X)$ is also denoted $\mathbb{E}$, and it may be noted that $\mathbb{E}\left[g\right] \circ \chi = \mathbb{E}\left[g \circ \chi\right]$. Then the operator T can be defined equally by $Tf = \mathbb{D}_V \, \mathbb{E}\left[fv\right]$, and so the invariant measures, if any, are the same. Note that $V = W$. Thus v is consistent with what w tells us about the phenotype, but sharpens it and extends it from $\chi(I)$ to the whole of X.

The first important link between forwards and backwards processes applies when there is a stable distribution of the population over classes, formally when the population measure μ_X is an eigenvector of $\tilde{U}$ with eigenvalue λ, and if a corresponding eigenfunction h of $\tilde{T}$ exists which is not μ_X-equivalent to zero. If h does represent per-capita reproductive value, then when it weights the population measure μ_X it should yield the class reproductive values τ. Formally, we will show that $h(x)\mu_X(dx)$ satisfies the defining feature of an invariant measure, namely that for arbitrary $f \in L^1(\mu_X, \mathbb{R})$,

$$\int f(x)h(x)\mu_X(dx) = \int (Tf)(x)h(x)\mu_X(dx) \tag{31}$$

It will suffice to consider an indicator function f of a measurable set A. The left hand side equals

$$\int_A h(x)\mu_X(dx) \tag{32}$$

In the right hand side we substitute using $Tf = \mathbb{D}_V \, \mathbb{E}\left[fv\right]$ and use the change of variables for Radon-Nikodym derivatives to obtain

$$\int (\mathbb{D}_V \, \mu_X)(x)h(x)\left(\int_A v(y)\mu_X(dy)\right)(dx) \tag{33}$$

As $V = \tilde{U}\mu_X = \lambda\mu_X$, it follows that $(\mathbb{D}_V \, \mu_X)(x) = (d\mu_X/dV)(x) = 1/\lambda$ as members of $L^1(V, \mathbb{R})$. Making this substitution, and by the method demonstrated in Section 3.2 we swap order of integration to obtain

$$\frac{1}{\lambda}\int_A \int h(x)v(y)(dx)\mu_X(dy) = \frac{1}{\lambda}\int_A \lambda h(y)\mu_X(dy) = \int_A h(y)\mu_X(dy) \tag{34}$$

as required. Thus if such a function h exists, then we can obtain an invariant measure by weighting the population measure μ_X with h, justifying the interpretation as per-capita reproductive value.

A linked result in the opposite direction is to begin with an invariant τ, and to show that the per-capita reproductive value $\mathbb{D}_V\,\tau$ satisfies the same relationship as h, namely that the value for a parent is proportional to the integral of the parental shares of the offspring's values, as in equation (26). The definition of invariance yields

$$\int f(y)\tau(dy) = \int \left(\mathbb{D}_V \int f(y)v(y)\mu_X(dy)\right)(x)\tau(dx) \tag{35}$$

By changing variables in the Radon-Nikodym derivative, and then swapping the order of integration, we can obtain

$$\int f(y)\tau(dy) = \int f(y)\int (\mathbb{D}_V\,\tau)(x)v(y)(dx)\mu_X(dy) \tag{36}$$

Now by choosing f to be the indicator function of an arbitrary measurable set A, this condition is effectively the definition of the Radon-Nikodym derivative of τ with respect to μ_X (Schechter, 1997, page 790, 29.10), with the inner integral on the right hand side as the derivative. Thus we may conclude that

$$(\mathbb{D}_{\mu_X}\,\tau)(x) = \int (\mathbb{D}_V\,\tau)(y)v(x)(dy) \tag{37}$$

At an equilibrium of class dynamics we have as before that $\mathbb{D}_{\mu_X}\,V = \lambda$, and so $\mathbb{D}_{\mu_X}\,\tau = \mathbb{D}_{\mu_X}\,V\,\mathbb{D}_V\,\tau = \lambda\,\mathbb{D}_V\,\tau$, and we obtain

$$\lambda(\mathbb{D}_V\,\tau)(x) = \int (\mathbb{D}_V\,\tau)(y)v(x)(dy) \tag{38}$$

Hence $\mathbb{D}_V\,\tau$ satisfies the same relationship (26) as defines h, though only over supp(V) and up to V-equivalence. In both cases, the per-capita reproductive value of a parent is proportional to the sum of its shares of the reproductive values of its offspring.

We summarise these two links. If an h exists, then there is a τ such that $\mathbb{D}_V\,\tau$ and h are equal up to V-equivalence. Similarly, if a τ exists, then there exists a member of $L^1(V,\mathbb{R})$ that satisfies the defining equation for h up to V-equivalence.

4.3. Useful theorems on existence and uniqueness

The conclusions of Section 3 apply whenever an invariant measure for T exists, justifying the concept of reproductive value up to that point. For further uses, we will require the existence of an eigenfunction of $\tilde{T}$ to act as per-capita reproductive values. Here we consider under what conditions reproductive value can be shown to exist. Three theorems of Krasnosel'skii (1964) relevant to the forwards process introduced in Section 4.1 are given first, and then two theorems of Rosenblatt (1971) for the backwards process from Section 3.1. The results are applied to examples in Section 4.5.

The results of Krasnosel'skii (1964) are on fixed points of linear operators in cones. The basic object is the function $v\colon X \to \mathcal{M}(X)$, and existence will be

studied in terms of its properties. $v(x)$ represents the offspring production of an individual parent in class x, and so $v(x)$ is necessarily non-negative, and we have also assumed that v is uniformly bounded. It follows that $\tilde{U}$ is a norm-continuous linear operator, which maps the cone of non-negative measures into itself. Theorem 2.6 (Krasnosel'skii, 1964, page 69) asserts that a completely continuous linear operator that is uniformly positive and has an invariant cone has at least one eigenvector in the cone. Complete continuity means that the operator is continuous and maps bounded sets into relatively compact sets. The extra properties, beyond our assumptions, we require to apply this result are compactness and uniform positivity. Compactness of $\tilde{U}$ follows if $\{v(x) : x \in X\}$ is compact, in view of our assumption that v is bounded. In some later examples, we will ensure this by the finiteness of the set. Uniform positivity requires that $|\tilde{U}^n m| \geq \alpha |m|$ for some n and $\alpha > 0$, for all m in the cone, and is satisfied if $v(x)(X) > \alpha$ for some $\alpha > 0$.

Theorem 2.7 of Krasnosel'skii (1964, page 71) applies to the case where $\{v(x) : x \in X\}$ is a subset of the set of probability measures. The conditions of the theorem are a weakly complete space whose unit sphere is weakly compact, a cone that allows plastering, and a linear operator that leaves the cone invariant; the conclusion is that such a linear operator has at least one eigenvector in the cone. Note that a cone generated by a bounded closed convex set allows plastering (Krasnosel'skii, 1964, section 1.4.4, page 34), and that the unit sphere of $\mathcal{M}(X)$ is weakly compact by the Banach-Alaoglu theorem. Thus if $\{v(x) : x \in X\}$ is a subset of the probability measures, then this theorem guarantees an eigenvector of $\tilde{U}$ in the cone.

The operator $\tilde{T}$ is defined on the Banach space $BM(X)$ of bounded measurable real functionals on X. The natural cone without further assumptions on v is the non-negative functions. Adjointness of $\tilde{T}$ and $\tilde{U}$ guarantee that if one is compact then so is the other, and so compactness of $\{v(x) : x \in X\}$ will guarantee compactness of $\tilde{T}$. Uniform positivity is harder to achieve in $BM(X)$, and Theorem 2.5 of Krasnosel'skii (1964, page 67) will often be more useful. It states that a linear completely continuous operator A which, for some non-zero element u such that $-u \notin K$, $u = v - w$ with $v, w \in K$, and for some $\alpha > 0$ and for some natural number p, satisfies the relation

$$A^p u \geq \alpha u \tag{39}$$

has an eigenvector in the cone with eigenvalue greater than or equal to $\sqrt[p]{\alpha}$.

There are two possible routes to stronger eigenvector results by applying the theorems to smaller cones. First, if v is continuous in the weak-star topology induced by $C(X)$, then the subcone of continuous functions is invariant under $\tilde{T}$, and we may be able to prove the existence of a continuous eigenvector. Second, if instead we assume that $v(x)$ for each x is absolutely continuous with respect to v_0, then $\tilde{T}$ maps $L^\infty(v_0, \mathbb{R})$ into itself, and we could establish an eigenvector in $L^\infty(v_0, \mathbb{R})$. But note that by switching from $BM(X)$ in this way we lose adjointness of $\tilde{T}$ and $\tilde{U}$, and so compactness would need to be shown separately.

Turning now to the backwards process, two main results will be employed. The first is from Rosenblatt (1971, Theorem 1, p101), and states that existence of an

invariant measure (which in addition is regular) is guaranteed if X is compact, and T maps continuous functions into continuous functions. Recall that $T : L^1(V, \mathbb{R}) \to L^1(V, \mathbb{R})$ is defined as $Tf = \mathbb{D}_V(\mathbb{E}[fv])$.

A general result about this condition is now derived. Begin by constructing a measure θ on the product space $X \times X$, with the product topology and product σ-algebra. Define θ as the distribution of parent-offspring pairs, which for rectangular sets $A \times B$ is given by

$$\theta(A \times B) = \int_A v(x)(B)\mu_X(dx) \tag{40}$$

We apply the Radon-Nikodym theorem to construct a derivative of θ with respect to the product measure $\mu_X \times V$, namely a function $k \in L^1(\mu_X \times V, \mathbb{R})$ such that

$$\theta(A \times B) = \int_{x \in A, y \in B} k(x, y)(\mu_X \times V)(dx \times dy) \tag{41}$$

and then define a probability measure on X as a function of X, $\beta \colon X \to \mathcal{M}(X)$, V-almost everywhere, by (an informal version is given in the brackets)

$$\beta(y)(A) = \frac{\int_A k(x, y)\mu_X(dx)}{\int_X k(x, y)\mu_X(dx)} \left(= \frac{\int_{x \in A} v(x)(dy)\mu_X(dx)}{\int_{x \in X} v(x)(dy)\mu_X(dx)} \right) \tag{42}$$

We then have

$$(Tf)(x) = \int f(y)\beta(x)(dy) \tag{43}$$

If this is to be continuous, then we need to have $f(y) = 0$ at points of discontinuity of β. Thus for Tf to be continuous for all continuous f, we require that $\beta(y)$ is continuous in y in the weak-star topology induced by $C(X)$.

The following are special cases of this general result, and so provide the existence of an invariant measure.

1. X is a finite set. For then all functions from X to $\mathbb{R}$ and from X to $\mathcal{M}(X)$ are continuous.
2. Each offspring class x is made by one parental class $z(x)$ with z continuous. Then we have $(Tf)(x) = f(z(x))$.
3. Each offspring class x is made by k parental classes $z_j(x)$ in per-capita amounts $q_j(x)$, with z_j and $q_j/\sum_j q_j$ continuous, for $j \in 1(1)k$. Let there be a density of population $m(x)$, which we also assume continuous, such that $\mu_X(dx) = m(x)dx$. Then we have

$$(Tf)(x) = \sum_j \frac{m(z_j(x))q_j(x)}{\sum_j m(z_j(x))q_j(x)} f(z_j(x)) \tag{44}$$

4. The density case. Suppose μ_X and $v(x)$ can be represented as

$$v(x)(dy)\mu_X(dx) = t(x)\sigma(x, y)\, dx\, dy \tag{45}$$

where $t(x)$ is the density of x as parents, and $\sigma(x, y)$ is the density of offspring of class y produced by one parent of class x. Then we have

$$(Tf)(y) = \frac{\int f(x)t(x)\sigma(x, y)dx}{\int t(x)\sigma(x, y)dx} \qquad (46)$$

This quotient is continuous in y provided $\sigma(x, y)$ is continuous in y for almost all x (whether or not f is continuous). This would be implied by the biological assumption that a parent cannot make offspring precisely in a class, but instead 'smears' offspring around 'intended' classes.

The second result is attributed by Rosenblatt (1971, Page 117) to Doob. An invariant measure is guaranteed if, in our notation, there exists a probability measure ϕ over X, an integer m and an $\epsilon > 0$ such that

$$\phi(A) \leq \epsilon \implies P_m(x, A) \leq 1 - \epsilon \quad \forall x \in X \qquad (47)$$

where $P_m(x, A)$ is the m-th iterated probability transition function. In the original Markov chain interpretation, this means that after long enough, there is no small set that is acquisitive for some x. In particular it must be the case that no set of ϕ-measure zero 'captures' all the descendants of an x. Capturing points are allowed, but they must be few enough that we can afford to assign an atom in ϕ so they are not of measure zero. Further, in a populated region of X there must be no point x which is the focus of nested sets, each of which directs descendant states in towards x, for then the innermost sets have smaller and smaller measure, and continue to capture all of their own offspring. Essentially, Doob's is a 'blurring condition'. In the biological interpretation, this means that as we trace back the ancestors of the individuals in a given class x, they must not become concentrated in a single class. Sexual reproduction, with mating across classes, will be helpful in meeting Doob's condition. Implications of meeting Doob's condition are discussed in Section 4.4.

Doob's condition ensures existence with finite X, for then we can choose the measure ϕ to attribute at least $\alpha > 0$ to each point. Then choosing $m = 1$ and selecting $\epsilon < \alpha$ renders the condition trivially true.

In the original forwards interpretation of the Markov process, it is easy to show that we could guarantee meeting Doob's condition by assuming that with some non-zero probability the next state is chosen independently of x and from a measure that is absolutely continuous with respect to the base measure. However, the biological interpretation looks backwards, and it is not meaningful to insist that a certain fraction of the population has its parent determined in such a way. It would be interesting to know of a biologically meaningful way of meeting Doob's condition in the case of infinite X.

The results of this section will be applied in Section 4.5.

4.4. Uniqueness

We now consider uniqueness of reproductive value, and begin with the invariant measure of the backwards process. Throughout this discussion, it will be assumed that the population under discussion is at a stable equilibrium of the distribution

over classes. Uniqueness is connected with notions of irreducibility of matrices. Essentially we will find we can define subsets of X over which there are unique invariant measures (up to multiplication by a scalar), and that we can characterise the set of invariant measures as linear combinations of those unique measures. I have not found a satisfactory discussion of the general case, perhaps because it is difficult. Here I will discuss the implications explained by Rosenblatt (1971, page 117) for the case where Doob's condition (equation 47) has been met. No doubt many features are shared by the general case.

The set of classes is divided into a conservative and a dissipative part. In the usual interpretation of the Markov process, a class in the dissipative subset has all of its successor states eventually in the conservative part, so the dissipative subset is eventually empty. In the biological, backwards, interpretation, a class in the dissipative subset has all its ancestors eventually in the conservative part, so that while there may be population in the dissipative part, its progeny eventually die out. An example of a dissipative subset would be sterile hymenopteran workers: they continue to exist each generation, but leave no progeny.

The conservative part of X is divided into a finite number of minimal ergodic subsets. An 'ergodic set' $A \subset X$ in this context is one for which the following condition holds for states in the conservative part of X:

$$P(x, A) = \begin{cases} 1 & x \in A \\ 0 & x \notin A \end{cases} \tag{48}$$

Such a set is minimal ergodic if no proper subset is also ergodic. An individual x in a minimal ergodic set A has an ancestry that never leaves A, and no individual in a conservative class outside A has any ancestry in A. They are therefore reproductively isolated subsets of the species. Even if there were no genetic differences initially, they would arise through drift, and probably also through genetic adaptations appropriate to each minimal ergodic set of classes separately.

While multiple ergodic sets are unlikely to be important in nature (unless one counts different species as different ergodic sets) they are important because they are likely to arise in models of adaptive evolution. For example, if there were ten classes, and each class produced offspring only of its own kind, then there would be ten ergodic sets. This could easily result if it was cheaper to make such offspring. Some of the examples applying uniqueness conditions in Section 4.5 have multiple ergodic sets.

It is an important result that a minimal ergodic set always has a unique invariant measure, up to multiplication by a scalar. This measure describes the reproductive value of all its subsets. The intermingling of all its subsets over the generations ensures uniqueness of reproductive value within a minimal ergodic subset.

A further complication is that it is possible for a minimal ergodic set B to be divided into a finite number of subsets $\{B_1, B_2 \ldots B_r\}$ such that the ancestor of $x \in B_1$ is in B_2, the ancestor of $x \in B_2$ is in B_3, and so on, and finally that the ancestor of $x \in B_r$ is in B_1. These sets thus move cyclically through the generations, and there are r distinct sets of ancestral paths which never intersect, each rotating through the r different sets of classes. One full treatment in the current

framework has classes defined by both age and phase, making r^2 classes in all. An extreme case in which only one set is populated is embodied in periodic cicadas, which appear as adults every so many years. The exact period is 13 or 17 depending on the species, and the phase differs within a species between geographical regions. See Williams & Simon (1995) for periodic cicadas. So-called 'annual cicadas' have shorter periods of 2–8 years, but usually all the possible phases are present, so there are no adult-free years even in one location.

Returning to the minimal ergodic sets themselves, each has a unique invariant measure defined on it, which extends to an invariant measure on the whole space that is zero elsewhere. But we can construct further invariant measures by taking any linear combination of those extended unique measures. For example, if the measure for A_i is τ_i, then $\tau_1 + \tau_3$ is also an invariant measure, and so is $2\tau_1 + \tau_2 + 5\tau_3$. All such linear combinations make up the invariant measures, and this family has a simple interpretation, which is deferred to Section 5.

The discussion of this subsection so far has been based on meeting Doob's condition. It would be useful to have parallel results for the more general case, which would presumably employ Choquet theory (Phelps, 2001).

Turning to the forwards process, the same general patterns arise in the ergodic sets for per-capita reproductive value, as they must owing to the links with the total reproductive value outlined in Section 4.2. Theorem 2.11 of Krasnosel'skii (1964, page 78) can help establish uniqueness. Note that for elements of general cones K, the inequality $f \leq g$ is to be understood as $g - f \in K$ (this coincides with the elementwise meaning when the cone of non-negative elements is considered). The first condition is that a linear operator A possesses the property of 'u_0-positiveness', namely that there exists a vector $u_0 \in K$ such that for each non-zero $x \in K$, there exist positive scalars α and β and integer n such that

$$\alpha u_0 \leq A^n x \leq \beta u_0 \tag{49}$$

The second condition is that K is reproducing, that is, every element in the space must equal the difference between some pair of elements in K. The third condition is that A has an eigenvector in K. If all three conditions are satisfied, then K contains a unique eigenvector of A, up to multiplication by a positive scalar. This result can be used for both $\tilde{U}$ in relation to population distributions, and for $\tilde{T}$ in relation to per-capita reproductive values.

4.5. Examples

We now turn to three examples to show how the criteria for existence and uniqueness can work. The forwards and backwards processes are defined and then attempts, usually but not always successful, are made to apply existence theorems. Even where none of the results can show existence, reproductive values are exhibited. Uniqueness is also studied, but less often holds. The reader's attention is drawn to the fact that the results of Krasnosel'skii (1964) and Rosenblatt (1971) employed through these examples are given in Section 4.3 for existence and in Section 4.4 for uniqueness.

As well as exhibiting application of the existence and uniqueness theorems, the examples show how the mathematical machinery introduced in the paper can be put to work. More biologically motivated examples are given in Section 8.

4.5.1. *Triangular offspring distributions*

Suppose $X = [0, 1]$, and classes $x \leq \frac{1}{2}$ each produce an upwards triangular distribution m_1 of offspring, while classes $x > \frac{1}{2}$ each produce a downwards triangular distribution m_2, formally

$$
v(x) = \begin{cases} m_1 & x \leq \frac{1}{2} \\ m_2 & x > \frac{1}{2} \end{cases} \qquad \text{where} \quad \begin{array}{l} m_1([0, y]) = y^2 \\ m_2([y, 1]) = (1 - y)^2 \end{array} \tag{50}
$$

We begin with defining the backwards process. Suppose the population distribution measure is μ_X. Then letting $p_1 = \mu_X([0, \frac{1}{2}])$, $p_2 = \mu_X((\frac{1}{2}, 1])$, $\bar{f}_1 = \int_{y \in [0, \frac{1}{2}]} f(y) \mu_X(dy)$, and $\bar{f}_2 = \int_{y \in (\frac{1}{2}, 1]} f(y) \mu_X(dy)$, we have

$$
(Tf)(x) = \frac{x p_1 \bar{f}_1 + (1 - x) p_2 \bar{f}_2}{x p_1 + (1 - x) p_2} \tag{51}
$$

This leads to continuity of (Tf) and so by Rosenblatt's condition to the existence of an invariant measure of the backwards process.

Doob's condition in equation (47) gives the same result. If necessary, replace μ_X with $\tilde{U} \mu_X$, to ensure it is positive on each half. Then write P as

$$
P(x, A) = \frac{x \mu_X(A \cap [0, \frac{1}{2}]) + (1 - x) \mu_X(A \cap (\frac{1}{2}, 1])}{x \mu_X([0, \frac{1}{2}]) + (1 - x) \mu_X((\frac{1}{2}, 1])} \tag{52}
$$

from which we know, as μ_X is positive on both halves of the interval, that

$$
P(x, A) \leq \max \left\{ \frac{\mu_X(A \cap [0, \frac{1}{2}])}{\mu_X([0, \frac{1}{2}])}, \frac{\mu_X(A \cap (\frac{1}{2}, 1])}{\mu_X((\frac{1}{2}, 1])} \right\} \tag{53}
$$

If we define ϕ in Doob's condition by

$$
\phi(A) = \frac{1}{2} \left(\frac{\mu_X(A \cap [0, \frac{1}{2}])}{\mu_X([0, \frac{1}{2}])} + \frac{\mu_X(A \cap (\frac{1}{2}, 1])}{\mu_X((\frac{1}{2}, 1])} \right) \tag{54}
$$

then we conclude that

$$
\phi(A) \leq \epsilon \Rightarrow P(x, A) \leq 2\epsilon \tag{55}
$$

Thus Doob's condition is satisfied with the remaining choices $m = 1$, and $\epsilon = 1/4$.

Turning to the forwards process, $\{v(x) : x \in X\}$ contains only two points, and so is certainly compact. $v(x)(X)$ is bounded away from zero, giving uniform positivity. Thus $\tilde{U}$ has an eigenvector, by Theorem 2.6 of Krasnosel'skii (1964), which is the equilibrium distribution of the population over classes. This is the measure with equal density across $[0, 1]$.

$\tilde{T}$ is continuous, but uniform positivity is impossible to achieve in the cone of non-negative bounded measurable functions, so instead we apply Theorem 2.5. This requires to find a positive power n of the completely continuous operator A and a suitable element u and a positive number α such that $A^n u \geq \alpha u$. We choose for simplicity the indicator function f of a non-trivial interval $[a, b] \subset (0, \frac{1}{2}]$. Calculation shows that

$$(\tilde{T} f)(x) = \begin{cases} b^2 - a^2 & x \leq \frac{1}{2} \\ (b - a)(2 - a - b) & x > \frac{1}{2} \end{cases} \tag{56}$$

and so $\tilde{T} f \geq (b^2 - a^2) f$. This satisfies Krasnosel'skii's theorem and shows existence of an eigenfunction. Hence per-capita reproductive value also exists, and turns out to be the constant function $h(x) = 1$.

Theorem 2.11 of Krasnosel'skii (1964) can be used to prove uniqueness. The condition of existence of an eigenvector is satisfied for $\tilde{T}$ and $\tilde{U}$, as we have just seen. For $\tilde{U}$, the cone of non-negative measures will be used, which is reproducing as required. We will consider $\tilde{T}$ as mapping $L^\infty(\mu, \mathbb{R})$ to itself, where μ represents Lebesgue measure on the interval, and consider the cone of non-negative elements, which is again reproducing. We now show u_0-positivity. Let $\tilde{f}_1 = \int 2yf(y)dy$ and $\tilde{f}_2 = \int 2(1 - y)f(y)dy$, and let $1_X \in BM(X)$ denote the function taking the value one everywhere. It is straightforward to show that

$$\tilde{U}^2 m = \tfrac{p_1 + 3p_3}{4} m_1 + \tfrac{3p_1 + p_2}{4} m_2 \tag{57}$$

$$\tilde{T}^2 f = \begin{cases} \frac{1}{4}\tilde{f}_1 + \frac{3}{4}\tilde{f}_2 & x \leq \frac{1}{2} \\ \frac{3}{4}\tilde{f}_1 + \frac{1}{4}\tilde{f}_2 & x > \frac{1}{2} \end{cases} \tag{58}$$

and so, that

$$\tfrac{1}{4}(m_1 + m_2) \leq \tilde{U}^2 m \leq \tfrac{3}{4}(m_1 + m_2) \tag{59}$$

$$\min\{\tfrac{1}{4}\tilde{f}_1 + \tfrac{3}{4}\tilde{f}_2, \tfrac{3}{4}\tilde{f}_1 + \tfrac{1}{4}\tilde{f}_2\}1_X \leq \tilde{T}^2 f \leq \max\{\tfrac{1}{4}\tilde{f}_1 + \tfrac{3}{4}\tilde{f}_2, \tfrac{3}{4}\tilde{f}_1 + \tfrac{1}{4}\tilde{f}_2\}1_X \tag{60}$$

The minimum is greater than zero because we deal only with non-zero f in showing u_0-positivity. Thus we obtain uniqueness in both cases. For $\tilde{U}$, this suffices. However, we had to consider $\tilde{T}$ acting on $L^\infty(\mu, \mathbb{R})$ to obtain u_0-positivity – all functions that are μ-equivalent to zero would have failed the test in $BM(X)$ as the minimum would equal zero. We extend the uniqueness on $L^\infty(\mu, \mathbb{R})$ to uniqueness on $BM(X)$ by noting that $\tilde{T}$ carries $BM(X)$ into $L^\infty(\mu, \mathbb{R})$, and so all eigenvectors in the larger space must lie within the smaller. Thus we conclude establishing uniqueness for both operators.

4.5.2. Half-shift

Assume there is a measure μ_X over classes $X = [0, 1]$, and that class x makes $x + \frac{1}{2}$ or $x - \frac{1}{2}$, whichever is in $[0, 1)$. Considering the backwards process, a continuous f gives discontinuous Tf unless $f(0) = f(1)$, so that Rosenblatt's condition fails.

Doob's condition also fails, as (employing the biological interpretation and looking backwards) each class's path of ancestors remains contained in a single point (apart from $x = 0$ and $x = \frac{1}{2}$ whose ancestry may also be shared with a second point, $x = 1$). Each such point would require an atom in ϕ to allow Doob's condition to be met, but every point in the interval would therefore require an atom, which is impossible.

In the forwards process, $\{v(x) \colon x \in X\}$ is a subset of the probability measures, and so we turn to Theorem 2.7 of Krasnosel'skii (1964). The cone of non-negative finite measures allows plastering, as it is generated by the bounded closed convex set of the probability measures, and so $\tilde{U}$ has an eigenvector in the cone. The eigenvectors of $\tilde{U}$ are measures m satisfying $m(A) = m(\frac{1}{2} + A)$ for some measurable $A \subset [0, \frac{1}{2})$ and also satisfying $m(\{1\}) = 0$. On the other hand, Krasnosel'skii (1964) offers little hope for $\tilde{T}$ as it is not compact (ruling out Theorems 2.5, 2.6 and 2.9), and as the unit ball in the space on which it is defined (namely $BM([0, 1])$ is not weakly compact (ruling out Theorems 2.7 and 2.8). Eigenfunctions of $\tilde{T}$ exist despite the failure to prove it, and are all functions h in $BM([0, 1])$ such that $h(x) = h(x + \frac{1}{2})$ for $x < \frac{1}{2}$, and $h(1) = 0$. These correspond to the fact that the population is simply swapped in two chunks, with each alternate generation being the same, with the exception of $x = 1$.

If we identify $x = 0$ and $x = 1$ to make X represent a circle, then Rosenblatt's condition now holds while Doob's continues to fail to hold for the backwards operator T. So far as the forwards process is concerned, Theorem 2.7 of Krasnosel'skii continues to ensure an eigenvector of $\tilde{U}$. As v is now continuous in the weak-star topology on $\mathcal{M}(X)$ induced by $C(X)$, $\tilde{T}$ becomes invariant on the subcone of continuous non-negative functions, but non-compactness remains a barrier. All of the eigenvectors persist into the circle, despite the problems in proving their existence on general grounds (which probably arise because the half-shift does not engage with the topology in a substantial way).

4.5.3. Split halves

Suppose the population is distributed as μ_X over $X = [0, 1]$. Suppose classes $x \le \frac{1}{2}$ produce a uniform distribution over $[0, \frac{1}{2}]$ while classes $x > \frac{1}{2}$ produce a uniform distribution over $(\frac{1}{2}, 1]$. We suppose μ_X is positive on both halves of the interval, for otherwise the example reduces to a simpler case. Then

$$(Tf)(x) = \begin{cases} \int_0^{\frac{1}{2}} f(y)\mu_X(dy)/\mu_X([0, \frac{1}{2}]) & x \le \frac{1}{2} \\ \int_{\frac{1}{2}+}^1 f(y)\mu_X(dy)/\mu_X((\frac{1}{2}, 1]) & x > \frac{1}{2} \end{cases} \tag{61}$$

and so is not in general continuous, causing Rosenblatt's condition to fail. Doob does give us this, however, as we may choose $m = 1$ and $\phi = \mu_X$. First defining $p_1(A) = \mu_X([0, \frac{1}{2}] \cap A)$ and $p_2(A) = \mu_X((\frac{1}{2}, 1] \cap A)$, and noting that

$$P(x, A) = (Tf_A)(x) = \begin{cases} p_1(A) & x \le \frac{1}{2} \\ p_2(A) & x > \frac{1}{2} \end{cases} \tag{62}$$

then we find

$$\mu_X(A) < \epsilon \quad \Rightarrow \quad p_i(A) < \frac{\epsilon}{\min\{\mu_X([0, \frac{1}{2}]), \mu_X((\frac{1}{2}, 1])\}} \tag{63}$$

hence we will have the required $P(x, A) \leq \epsilon$ provided

$$\epsilon < \left(1 + \frac{1}{\min\{\mu_X([0, \frac{1}{2}]), \mu_X((\frac{1}{2}, 1])\}}\right)^{-1} \tag{64}$$

Thus Doob gives us an invariant measure. There is a whole continuum of asymptotic population distributions, in which the distribution in each half is uniform while the weight in each half depends on the initial allocations.

Turning to the forwards process, $\{v(x) : x \in X\}$ consists of only two non-zero points, so $\tilde{U}$ is completely continuous and uniformly positive: hence Theorem 2.6 of Krasnosel'skii (1964) shows that an equilibrium distribution of classes exists. Indeed, we could apply the result to each of the narrower cones of measures

$$K_1 = \{m : m \geq 0, \text{supp}\, m \subset [0, \frac{1}{2}]\} \tag{65}$$

$$K_2 = \{m : m \geq 0, \text{supp}\, m \subset [\frac{1}{2}, 1], m(\{\frac{1}{2}\}) = 0\} \tag{66}$$

to show the existence of an equilibrium distribution of classes within each cone. Note that under the norm topology, both sets are convex and closed, as required of cones. Uniqueness within each cone is trivial, as all measures in K_i are carried by $\tilde{U}$ immediately to the eigenvector in K_i. Within the larger cone of non-negative measures, every positive linear combination of these two eigenvectors is also an eigenvector.

The adjoint operator $\tilde{T}$ has two invariant cones

$$L_1 = \{h \in BM(X) : h((\frac{1}{2}, 1]) = \{0\}\} \tag{67}$$

$$L_2 = \{h \in BM(X) : h([0, \frac{1}{2}]) = \{0\}\} \tag{68}$$

Again, this shows existence within each cone. Uniqueness again follows trivially, as $\tilde{T}$ carries every function in L_i immediately to the eigenfunction in L_i. Within the larger cone of non-negative bounded measurable functions, every positive linear combination of these two eigenfunctions is also an eigenfunction.

5. Interpretation of reproductive value

We first turn to the interpretation of total reproductive value, as embodied in an invariant measure of the backwards process, and go on to consider the interpretation of per-capita reproductive measure, as embodied in an eigenfunction of the operator $\tilde{T}$. We learnt in Section 3.1 that the mathematical development frequently defines the invariant measure τ within a single generation, provided all subsets of classes with no offspring also have no parents. While reproductive value has a biological interpretation over one generation, its most important biological interpretation relies on an assumption that the same measure is invariant over a number

of generations. Essentially we will assume in this discussion that the population we are discussing maintains the same relative distribution of classes over time.

We defined an 'ergodic set' in Section 4.4 as a set A of classes such that all ancestry of A belongs to A, and no other ancestry belongs to A (except perhaps from classes that have no descendants themselves in the long term, the 'dissipative' classes). A minimal ergodic set has no proper subsets that are also ergodic. We saw that a minimal ergodic set has a unique invariant measure. The biological interpretation is to pick an individual, and then one allele within that individual, in one generation, and find the distribution of the allele's ancestors over classes in a large set of consecutive distant generations. If the generations are sufficiently numerous and sufficiently distant, then the distribution of the ancestors across classes can be represented as a probability distribution or measure over the classes. Two alleles picked from the same minimal ergodic set will give rise to the same ancestral measure.

If the whole of X is a minimal ergodic set, then this unique measure therefore establishes completely the relative values of all the different classes as ancestors of distant generations. Some subsets of classes, such as sterile workers, may even have measure zero. This justifies the name 'reproductive value', and shows the importance of the concept in natural selection. The Price equation (22) shows that what happens to a class of individuals has a significance for natural selection that is proportional to its reproductive value, and that individuals are selected to value offspring according to their per-capita reproductive value.

Now suppose there is more than one minimal ergodic set. We modify our thought-experiment by choosing the individual and one of its alleles through some random process. If by this process the chosen allele might come from more than one ergodic set, then the distribution of the ancestral state will be some mixture of the invariant measures for each minimal ergodic set, and by choosing the probabilities appropriately, we can obtain any convex combination of the unique invariant measures. Thus the family of invariant measures are all those measures which can provide the distribution of distant ancestry from some given process of random choice of an allele in an individual in this generation.

The non-uniqueness arises because ancestry provides no way to establish the relative importance of two subsets of classes whose ancestry never intersects. Thus all distinct relative importances produce distinct invariant measures. Such subsets are as separate as different species, because there is no gene flow among them. An extreme caste system, or complete geographical separation, could in principle produce such subsets within a species.

However, not all of these invariant measures will fulfil the fourth and crucial role of reproductive value, namely as a maximand of adaptive evolution. Explicit links to optimisation programs are made in parallel papers (Grafen, 2002, 2006), where there is enough work to do with them to justify introducing the notation. Explicit optimisation is also shown in the examples in Section 8, where less general results are required. Here, an example will show why not all invariant measures produce a maximand. Suppose there are two classes x and y, and an individual produces exactly one offspring of its own class and none of the other. The two classes perpetuate themselves and remain in equilibrium. Then the invariant measure τ can

place an arbitrary weighting on x and the remainder on y, for whatever chances we place on choosing classes in the offspring will be the chance that the parent is of those classes. But further suppose that a class x parent has the option of producing 0.7 class y offspring, and that a class y parent could produce 0.9 class x offspring, but that neither of these options is taken up at equilibrium. Then $\tau(\{x\})$ and $\tau(\{y\})$ are the class reproductive values, and $\mu_X(\{x\})$ and $\mu_X(\{y\})$ are the masses of individuals in the classes. It follows that the per-capita reproductive values are

$$h(x) = \frac{\tau(\{x\})}{\mu_X(\{x\})} \quad \text{and} \quad h(y) = \frac{\tau(\{y\})}{\mu_X(\{y\})} \tag{69}$$

The two classes of parents are acting optimally in continuing to produce their own kind only if these conditions hold

$$h(x) \geq 0.7h(y) \tag{70}$$
$$0.9h(x) \leq h(y) \tag{71}$$

This would limit the ratio of per-capita reproductive values to lie between 7/10 and 10/9. In general, all options not taken up will place restrictions on which of the invariant measures produce maximands.

Is it possible that this kind of argument might rule out all of the invariant measures? Indeed it is, and will occur when the behaviour is not optimal. Let us amend the previous example, and suppose that an individual in class x could have made 2.5 offspring in class y, while an individual in class y could still make 0.9 offspring in class x. Then the optimal behaviour would be for each class to make the other, producing a higher rate of increase for each lineage, growing by a ratio of 1.5 each generation compared to the static population of the original phenotype. It is appropriate that none of the invariant measures will produce a maximand.

We now turn to the interpretation of per-capita reproductive values as represented by a solution h to equation (26), and restrict ourselves initially to the case where there is only one minimal ergodic set in X. In populated regions of X, $h(x)$ is just the total reproductive value of class x, divided by the population size at x. This ratio is however undefined in unpopulated regions, and yet h has a crucial interpretation there. Suppose we begin with an individual at x. Then we know from the invariant measure what the class-distribution of its descendants will eventually be, and $h(x)$ represents how many of those descendants there will be. As individuals in every class x produce the same eventual class-distribution, $h(x)$ represents the ratio of the numbers of descendants produced by adults at each x. The significance of this extension beyond populated regions arises when considering the fate of mutants with low penetrance. A mutant may cause an individual to place offspring outside the populated regions, but because of the low penetrance, the descendants of those 'outsiders' will have regained the populated regions before the deviant behaviour occurs again. The value of $h(x)$ for those outsider offspring evaluates their descendants, as shown formally in equation (27). Thus the wider definition of per-capita reproductive value is essential when dealing with mutants that place offspring outside the regions populated by the common phenotype.

It is important to stress that total reproductive value and per-capita reproductive value depend on different information. Total reproductive value, embodied in the invariant measure τ, is obtained from information on $w(i)$ alone, that is, from information about the classes that are occupied. By contrast, the per-capita reproductive value h depends on knowing $v(x)$ for all x, which includes what would be done by individuals in unoccupied classes. The per-capita reproductive value in unoccupied classes must be calculated from assumption, as 'observation' can produce only the undefined quotient zero divided by zero.

6. Equilibrium under natural selection with classes

The existence of classes creates a question about how evolutionary equilibrium is to be defined. Two possibilities are described in this section, and then using the second, two important results are proved about natural selection in the presence of classes.

6.1. Clonal growth

The simplest approach is based on the idea of a completely dominant allele, which brings about a new phenotype in every bearer. The bearers thus grow as a clone would, and the complication of classes means keeping track of the distribution of the clone over the classes, and finding its intrinsic growth rate. The key point is that when averaging across the new strategy's success in the different classes, the average is weighted by the distribution of classes brought about by the new strategy's own behaviour.

We therefore define a Markov operator $\tilde{U}_a \colon \mathcal{M}(X) \to \mathcal{M}(X)$ to represent the evolution over one generation of the distribution over X of a clone of a-strategists whose distribution of offspring classes is given by v_a. Formally,

$$\tilde{U}_a(m) = \int v_a(x) m(dx) \tag{72}$$

The spectral radius of the operator will be denoted $\rho(\tilde{U}_a)$. In fact this operator is the operator $\tilde{U}$ of the forwards process, but recognising the dependence on a given phenotype a.

If we assume that the population as a whole is at a putative equilibrium and has reached a stable population density with monomorphic strategy a, then a condition for equilibrium is that no strategy could spread, formally that $\rho(U_b) \leq \rho(U_a)$ for all feasible strategies b. This inequality can be used as the basis for an optimisation program with the spectral radius as maximand. See Grafen (1998) for an example of such an optimisation program, but in a simpler case with finite X.

Reproductive value plays no obvious role in this equilibrium concept.

6.2. Stubblefield's 'tracer-allele' method

The alternative approach (Seger & Stubblefield, 2002) is to consider a mutant that has very low penetrance. Thus, it plays the existing strategy most of the time, and

occasionally plays a new strategy. The difference this makes is that the new strategy is played in a distribution of classes that corresponds to the distribution of the population as a whole, rather than the distribution that would come about through the actions of the new strategy itself.

As the mutant is played in the same distribution of classes as the population, a p-score is selected according to the sign of $\mathbb{I}_\tau (\pi' - \pi)$. Recall from equation (21) that

$$\mathbb{I}_\tau (\pi' - \pi) = \mathbb{E}\left[p\left(\mathbb{F}_W^\tau w - \mathbb{E}\left[\mathbb{F}_W^\tau w \mid \chi \right] \right) \right] \tag{73}$$

If a population is such that no p-score would spread, it follows that the right hand factor in the expectation must equal zero as a member of $L^1(\mu_I, \mathbb{R})$, and the converse also holds. Formally,

$$\mathbb{F}_W^\tau w = \mathbb{E}\left[\mathbb{F}_W^\tau w \mid \chi \right] \Leftrightarrow \text{no p-score can spread} \tag{74}$$

The interpretation is simple: there is no natural selection exactly when each individual has the same scalar evaluation of its reproductive output as the other individuals in the same class (apart from a possible set of individuals of measure zero). This is the formal statement for an arbitrary set of classes as was noticed for finite classes by Fisher (1930), Taylor (1990) and others, to the effect that if fitness differences are related to class but not to phenotype, then weighting by reproductive value gives no net selection. With any other weighting, two alleles with identical phenotypic effects could be differentially selected simply as a result of being distributed differently over the classes.

Equation (74) is the condition that all extant phenotypes should be in selective equilibrium, which in the parallel analysis without classes Grafen (2002) calls 'no scope for selection'. The 'potential for selection' is measured by the success of a non-extant phenotype a that usually produces the same offspring distribution v as the population as a whole, but with very low probability produces the distribution v_a. Assuming that the descendants return to the population distribution before the mutant is expressed again, we can use equation (27) to write the condition that no such mutant could spread:

for all feasible mutants a

$$\iint h(y)v_a(x)(dy)\mu_X(dx) \le \iint h(y)v(x)(dy)\mu_X(dx) \tag{75}$$

The implications depend very much on the set of possible mutants. The general expression allows arbitrary constraints that link behavior in different classes; but if behaviour in all classes can evolve separately, then we have the simpler

for all feasible mutants a and classes x

$$\int h(y)v_a(x)(dy) \le \int h(y)v(x)(dy) \tag{76}$$

These are the two basic results for selection in the presence of classes.

6.3. *Comparison of the concepts*

The logical basis of the difference between the clonal growth and tracer-allele equilibrium concepts is how they weight the classes when averaging the effects of phenotypes across the different classes. Clonal growth assumes the mutant allele has the distribution over phenotypes produced by a clone showing the mutant strategy, whereas a mutant allele will usually have a more complex relationship to the mutant strategy: to give only two simple examples from diploid genetics, it could be a recessive allele or it could show partial penetrance. Even a dominant allele would deviate from the clonal case once it was frequent enough for homozygotes to arise. Tracer-alleles assume that the mutant allele's distribution over classes is identical to the population's existing distribution. While this would follow from extremely low penetrance, or from a simple constant factor of advantage in reproduction in all circumstances per copy of the allele, it is otherwise most unlikely. Other distributions of the mutant allele over classes are highly likely to be relevant in real cases. However, these are two natural possibilities that have been used in the literature (Seger & Stubblefield, 2002). In the rest of the paper, it is the tracer-allele method that will be employed.

There are reconciliatory conditions in which these conditions are the same for mutants close to the incumbent, and Grafen (1998) gives an example in which the two conditions are equivalent for all mutants when a population is at a selective equilibrium.

The tracer-allele approach is more convenient to apply in evolutionary models because once reproductive values $h(x)$ have been worked out under the incumbent phenotype, a simple weighting of offspring classes allows the evaluation of the success of any mutant phenotype, so long as we are willing to assume low penetrance. This implies a simple trade-off between offspring classes that is the same for adults in every class, and that can be applied in one aspect of the phenotype independently of choices in other aspects.

There is a general biological defence of using the tracer-allele equilibrium concept to investigate the effects of selection on phenotypic traits. This concept uses little information about genetics, but nevertheless allows results to be obtained. Full population genetic models use more information, and clearly some full genetic model must be right in any particular situation. The main difficulty with full models is that the extra genetic information will usually be unknown in any particular case, and furthermore will also be different in every particular case. For example, a model about sex ratio using the tracer-allele concept provides admittedly tentative results, but they apply to a wide variety of species. A full model would require information that was different for each species, and even if the information were available, would produce predictions that were different. Thus the approximate applicability of the tracer-allele concept is close to a necessary condition for general biological explanations. If genetic details are truly required, then such general explanations do not exist. The optimisation programs attached to the phenotypic concepts also provide an interpretation of the conclusions that makes sense of the biology.

The argument between game theorists and population geneticists over the relative value of strategic models and explicit genetic models cannot be reviewed

here, and will certainly continue. A major purpose of the formal Darwinism project (Grafen, 2002, 2006, and the present paper) is to put the strategic models on an equal footing in terms of mathematical rigour, so that choices can be made on the grounds of biological utility.

The next two sections apply the tracer-allele approach, first to expound Fisher's use of reproductive value, and then to apply the mathematical machinery developed in this paper to some examples.

7. Fisher's four uses of reproductive value

One principle aim of the paper is to make explicit Fisher's concept of reproductive value as an evolutionary maximand. In this section, which is intended to be accessible to biologists with only a little mathematical notation, Fisher's uses of reproductive value in his 1930 book are reviewed. Page numbers are taken from the Variorum edition published in 2000. Then the links are made to the formalism established in earlier sections. The reader is reminded that reproductive value assigns a numerical value to individuals and to subsets of the population, representing their importance in evolutionary processes.

Fisher first employs the concept on pages 27 to 29 in relation to the Euler equation and age-structured populations (for a more recent treatment see Charlesworth, 1994). On page 29, he makes the point, in the same context, that using reproductive value appropriately over one generation is the equivalent of looking an indefinite number of generations ahead in order to obtain an asymptotic measure of fitness. In deriving the fundamental theorem of natural selection, he asserts on page 35 that individuals should be weighted by their reproductive value when gene frequencies are measured. On page 73, Fisher declares in comparing the strength of natural selection in larvae and adults first that one should count not number of bearers but rather their summed reproductive value, and second that weighting by reproductive value in this way brings about comparability between the two groups.

The only explicit use as a maximand comes in pages 141 to 143 in the famous sex ratio argument, but here many logical steps are taken. The total reproductive values of all males and of all females are calculated, and then the per-capita reproductive values. These are attributed as the value of a son and a daughter, and the sum of the shares of a parent in the reproductive values of its offspring is identified with the reproductive value of the parent itself. It is then assumed that selection will cause this reproductive value to be maximised within the actions available to the individual. Further, uncertainty is taken into account when the probability-weighted arithmetic average is taken over possible reproductive values.

The various manipulations exhibit a sophisticated if implicit structure. It is now shown how the machinery of the present paper provide formal justifications for most of these manipulations, and in a very general setting. The exception is averaging over uncertainty, which must be deferred. Reproductive value is thus shown to be a central concept in natural selection in the presence of classes.

Fisher (1930) used reproductive value in four formal ways that are illustrated by the roles played by reproductive value in the Price equation with classes. Equations

(22) and (23) are expressed in terms of h as follows:

$$\int h(x)\big(\pi'(x) - \pi(x)\big)\mu_X(dx) = \mathbb{E}\left[\mathbb{C}\left[p, \int h(x)w(\cdot)(dx) \mid \chi\right]\right] \quad (77)$$

$$\int h(x)\big(\pi'(x) - \pi(x)\big)\mu_X(dx) = \mathbb{C}\left[p - \mathbb{E}[p \mid \chi], \int h(x)w(\cdot)(dx)\right] \quad (78)$$

The equations need to be explained for readers who have skipped the mathematical sections, who can understand 'p-score' to mean 'gene frequency'. $h(x)$ is the per-capita reproductive value of an individual in class x. $\pi'(x)$ and $\pi(x)$ are the mean p-score next generation and this generation among individuals in class x, and μ_X represents the population distribution over classes in the parental generation. Thus the left hand side represents a population-wide average change in p-score from this generation to the next, weighting by reproductive value. On the right hand side, the integral represents the reproductive-value-weighted evaluation of one individual's production of offspring – or more accurately, of her appropriate share of them, according to the fraction of each offspring's genes she contributed. The first right hand side is the average over classes of the covariance across individuals within a class between p-score and that integral. The second right hand side is the covariance over all individuals between the deviation of p-score from class mean p-score, and that integral.

Fisher's first and second uses are that reproductive value provides the weights in aggregating gene frequencies into a single gene frequency, either by individual weight or by class weight. The use of h is in the left hand side of equations (77) and (78), where $h(x)$ is the weight of an individual in class x and $h(x)\mu_X(dx)$ is the total weight of class x. These weights have the special property that when there is no selection within classes, indicated by the covariances in the right hand sides all taking the value zero, there is no change in the mean gene frequency. Aggregating gene frequencies must be done with very special weights to have this property, and this is one of the important properties of per-capita reproductive values (this result is shown formally in Section 6.2).

The third use is in the construction of an individual's reproductive value, when reproductive values are used to weight the sum of shares of offspring produced of each class. This is shown in the right hand sides of equations (77) and (78), where $h(x)$ is used to weight the gametic contributions by an individual to offspring of type x.

The fourth use of reproductive value is as a maximand, a function individuals are selected to maximise. This use can be seen in the position of the individual's weighted sum of its shares in the reproductive values of its offspring, as the target of selection in the Price equation (77 and 78). This corresponds to the role of number of offspring in the standard Price equation (Price, 1970), to expected relative number of offspring in the Price equation with uncertainty (Grafen, 2002), and to expected relative inclusive fitness in the Price equation with uncertainty and effects on relatives (Grafen, 2006). Once there are various classes of offspring, then aggregation is required to find a single maximand. It is the combination of weighting gene frequencies by reproductive value, and summing offspring number

weighted by reproductive value, that allows the conclusion that a p-score positively correlated with aggregated offspring number will increase.

So far the target of selection has been the sum of the parent's shares in its offspring's reproductive value. In view of equation (26), which defines reproductive value in a uniform population as the sum of its shares in the reproductive value of its offspring, we can understand the parent's own reproductive value as the target of selection, and regard it as a generalisation of counting offspring, giving weights according to class.

The second major result can also be interpreted in Fisherian terms. This is the condition for a strategy with reproductive output v to be proof against invasion: for all feasible mutants a

$$\iint h(y)v_a(x)(dy)\mu_X(dx) \leq \iint h(y)v(x)(dy)\mu_X(dx) \qquad \text{(75, repeated)}$$

Each side is a double integral that first adds up the reproductive value of offspring of an individual in class x, and then adds those up weighting by the distribution of adults in the different classes, yielding a total reproductive value for v_a on the left, and for v on the right. This clearly shows that to be uninvasible, v must attain the maximum of that double integral, over feasible possibilities. The optimisation of reproductive value as a condition for evolutionary equilibrium, used by Fisher in his sex ratio argument, is thus exhibited formally.

For both results, weighting by per-capita reproductive value reduces the possible complexity of classes considerably. Offspring classes each have a weight, and the quantity to be maximised is the sum of those weights over the offspring produced. Thus there is a simple tradeoff between all pairs of offspring classes, and furthermore that tradeoff is the same for all parental classes. The formalism therefore shows how the assumption of low penetrance, and the assumption of one common type faced with possible rare mutants, together simplify the operation of natural selection in the presence of classes and permit a simple optimisation view.

Fisher nowhere gives a formal argument for employing reproductive value as a maximand when there are classes present in the population. The Price equation, however, provides a framework in which reproductive value plays a central role, and which unites and fully justifies Fisher's various uses of the concept in a very general setting.

8. Examples

The examples in this section show the theory at work. The first example is Fisher's sex ratio argument. We follow Taylor (1990) in providing a treatment in which the derivation and application of reproductive value are fully included in the formal arguments. The power of the theory is shown by various extensions. The second model is of parental care, in which resources are distributed to individuals on the basis of size. A technical point here is a further result of Rosenblatt (1971), extending his condition to non-compact X. The third example is geographical.

In the examples, we shall assume in the notation of Section 4 that the population measure over classes is μ_X, and that the aggregate production of offspring over X is V.

Optimisation programs are introduced explicitly here. It is convenient to state here without proof two very simple results about linear programming in infinite dimensions. The literature (e.g. Luenberger, 1997; Anderson & Nash, 1987) seems to provide no simple and suitable general results, as it is concerned with more complicated problems.

For the first result, we assume Y is compact Hausdorff which with its Borel sets forms a measurable set, $K > 0$, and f, g are measurable functions from Y to $\mathbb{R}$ satisfying $f \geq 0$, $f \neq 0$ and $g(x) > 0$ for all x. Consider the optimisation program for non-negative finite real measures over Y,

$$\mu \quad \max \int f(x)\mu(dx),$$

$$\int g(x)\mu(dx) \leq K \tag{79}$$

Let $\lambda = \sup\{\frac{f(x)}{g(x)}\} \in (0, \infty]$. Then we claim that

$$\mu\left(\left\{x : \frac{f(x)}{g(x)} = \lambda\right\}\right) = \mu(Y) \Leftrightarrow L\mu \text{ solves program (79) for some scalar } L > 0 \tag{80}$$

Note that this result requires measurable functions f and g defined everywhere, and not merely belonging to some L^1; and I am grateful to Dr Matthew Daws for the observation that the set of maximising values is measurable as it is the inverse image of a measurable set under a measurable function.

For the second result, we assume Y is compact Hausdorff which with its Borel sets forms a measurable set, μ is a positive real finite measure on Y, $f \in L^1(\mu, \mathbb{R})$, $f \geq 0$, $f \neq 0$, and $K > 0$. Consider the optimisation program for instruments $k \in L^\infty(\mu, \mathbb{R})$

$$k \quad \max \int f(x)k(x)\mu(dx),$$
$$k(x) \geq 0$$
$$k(x) \leq 1$$
$$\int k(x)\mu(dx) \leq K \tag{81}$$

Then let $Q(c) = \{x : f(x) > c\}$ and $R(c) = \{x : f(x) = c\}$. Then $\mu(Q(c))$ and $\mu(Q(c) \cup R(c))$ are non-increasing functions of c. Suppose $\mu(Q(0)) \geq K$. Let $c^* = \inf\{c : \mu(Q(c)) < K\}$. Then we claim that a necessary and sufficient condition for k to be a solution to the program (8.1) is

$$\int k(x)\mu(dx) = K \text{ and } \mu\text{-a.e.} \begin{cases} k(x) = 1 & x \in Q(c^*) \\ 0 \leq k(x) \leq 1 & x \in R(c^*) \\ k(x) = 0 & x \notin Q(c^*) \cup R(c^*) \end{cases} \tag{82}$$

Armed with these results, we now tackle three examples.

8.1. A sex ratio model

The only model in which Fisher explicitly used reproductive value as a maximand was his sex ratio argument. Edwards (1998) claims that the argument was not original with Fisher. The reproductive value aspects to be brought out in the present treatment show a central part of the rigorous argument which I do not believe was made before Fisher in 1930. In particular, the need to show that the reproductive value of all males equalled the reproductive value of all females, and indeed the conceptual framework in which such a statement can even be formulated, were not to my knowledge appreciated by earlier authors. Until Mendel's results became widely known, biologists did not know the crucial fact for this argument that the two parents contribute equally to each offspring, and indeed this is not true for sex chromosomes in diploids, or at all for haplodiploids. It is at least possible that Darwin (1871) withdrew his sex ratio argument in making the second edition of the *Descent of Man* because he saw this lacuna in the argument of the first edition.

It is fitting to begin by making Fisher's argument of equal total reproductive values. The situation is one in which the sexes are distinct and parents choose the sex of offspring. Class therefore determines sex, and so we may write the sets of male and female classes as M and F, with $M \cup F = X$ and $M \cap F = \emptyset$.

Making the same assumption as Fisher that each offspring receives equal contributions from a father and a mother, it follows that the total reproductive output of males equals the total output of females, where the equality holds for the whole distribution across classes. We require to show that this equality of total reproductive output implies equality under the invariant measure τ, or formally

$$\int_M v(x)\mu_X(dx) = \int_F v(x)\mu_X(dx) \quad \Rightarrow \quad \tau(M) = \tau(F) \tag{83}$$

We will prove that this must be true on the supposition that τ is an invariant measure, without proving that one exists. By definition an invariant measure satisfies

$$\mathbb{I}_\tau f = \mathbb{I}_\tau Tf \qquad \forall f \in L^1(V, \mathbb{R}) \tag{84}$$

By definition, $Tf = \mathbb{D}_V \mathbb{E}[fv]$. Let us choose f to be in turn f_M and f_F, the indicator functions of M and F. Then we have

$$\tau(M) = \mathbb{I}_\tau f_M = \mathbb{I}_\tau \mathbb{D}_V \mathbb{E}[f_M v] = \mathbb{I}_\tau \mathbb{D}_V \int_M v(x)\mu_X(dx) \tag{85}$$

$$\tau(F) = \mathbb{I}_\tau f_F = \mathbb{I}_\tau \mathbb{D}_V \mathbb{E}[f_F v] = \mathbb{I}_\tau \mathbb{D}_V \int_F v(x)\mu_X(dx) \tag{86}$$

But the final term in each line is equal by the hypothesis of equation (83), and so we have as required that $\tau(M) = \tau(F)$. Thus Fisher's equality result is true in an extremely general setting.

The equality result just obtained will be used below, but first we show how the argument can be generalised beyond simple diploidy, and study the 'arbitrary ploidy' model of Grafen (1986), which includes diploidy, haplodiploidy and haploidy as special cases. Assume that all males share the same ploidy and all females share the same ploidy, but these may be different. Females contribute γ_{FF}-ploid gametes to daughters and γ_{FM}-ploid gametes to sons. Males contribute γ_{MF}-ploid

gametes to daughters and γ_{MM}-ploid gametes to sons. We aim to find the class reproductive values of females and males, still retaining the assumption of discrete non-overlapping generations.

Define $k \in L^1(V, \mathbb{R})$ by $k = \mathbb{D}_V \int_F v(x)\mu_X(dx)$. Then $k(y)$ equals the fraction of successful gametes in type y offspring that come from females. The ploidy assumptions show we must have

$$k(y) = \begin{cases} \frac{\gamma_{FF}}{\gamma_{FF}+\gamma_{MF}} & y \in F \\ \frac{\gamma_{FM}}{\gamma_{FM}+\gamma_{MM}} & y \in M \end{cases} \tag{87}$$

We apply the definition of invariance for τ to the indicator function f_F, to obtain

$$\tau(F) = \mathbb{I}_\tau \mathbb{D}_V \int_F v(y)\mu_X(dy) = \mathbb{I}_\tau k \tag{88}$$

$$= \frac{\gamma_{FF}}{\gamma_{FF} + \gamma_{MF}}\tau(F) + \frac{\gamma_{FM}}{\gamma_{FM} + \gamma_{MM}}\tau(M) \tag{89}$$

showing that

$$\frac{\tau(F)}{\tau(M)} = \frac{\frac{\gamma_{FM}}{\gamma_{FM}+\gamma_{MM}}}{\frac{\gamma_{MF}}{\gamma_{FF}+\gamma_{MF}}} \tag{90}$$

which has a nice interpretation in words as

$$\frac{\text{reproductive value of all females}}{\text{reproductive value of all males}} = \frac{\text{fraction of male genome from mother}}{\text{fraction of female genome from father}} \tag{91}$$

This argument includes haplodiploidy with $\gamma_{FF} = \gamma_{FM} = \gamma_{MF} = 1$ and $\gamma_{MM} = 0$. Note that, as with the simple diploidy result, the results hold even if there are subclasses within F and M with their own further subdivisions of reproductive value. This result confirms that of Grafen (1986), obtained with informal methods.

8.1.1. Fisher's original argument

In Fisher's original argument, $X = M \cup F$ and M and F have one element each. A parent's production of male and female offspring, $g(M)$ and $g(F)$, was limited by the investment required according to a linear constraint of the form $c_M g(M) + c_F g(F) \leq K$, where the per-capita costs are c_M and c_F. The total reproductive values of males and females are equal to each other, as we have just seen, and so equal to $\frac{1}{2}$. We make explicit Fisher's implicit assumption that we are considering a rare mutant in a very large population whose incumbent strategy is not changing from one generation to the next. The per-capita reproductive values are therefore

$$\frac{1}{2\mu_X(M)} \quad \text{and} \quad \frac{1}{2\mu_X(F)} \tag{92}$$

The optimisation program for an individual choosing offspring numbers is therefore

$$g(M), g(F) \quad \max \quad \frac{g(M)}{2\mu(M)} + \frac{g(F)}{2\mu(F)},$$

$$g(M) \geq 0$$
$$g(F) \geq 0$$
$$c_M g(M) + c_F g(F) \leq K \tag{93}$$

We introduce Lagrangean multipliers λ, γ_M and γ_F, and the Lagrangean itself as

$$L = \frac{g(M)}{2\mu(M)} + \frac{g(F)}{2\mu(F)} + \gamma_M g(M) + \gamma_F g(F) - \lambda(c_M g(M) + c_F g(F) - K) \tag{94}$$

The Lagrangean is unconstrainedly maximised by the instruments, and the resource constraint will always be met with equality. Thus we write the conditions for a constrained optimum as

$$\frac{1}{2\mu(M)} - \lambda c_M + \gamma_M = 0 \qquad \text{C.S.} \begin{cases} \gamma_M \geq 0 \\ g(M) \geq 0 \end{cases}$$

$$\frac{1}{2\mu(F)} - \lambda c_F + \gamma_F = 0 \qquad \text{C.S.} \begin{cases} \gamma_F \geq 0 \\ g(F) \geq 0 \end{cases} \tag{95}$$

where C.S. denotes complementary slackness (i.e. at least one inequality holds with equality).

As is typical in ESS and optimality arguments, we are going to use properties of the maximisation to draw conclusions not about the maximising response, but about the population values $\mu_X(M)$ and $\mu_X(F)$. If all individuals have the same costs, then their solution to this optimisation program will be the same. If $\gamma_M > 0$, then by complementary slackness no males are made by optimising agents, which precludes an equilibrium. Thus at an equilibrium we must have $\gamma_M = 0$ and by a parallel argument $\gamma_F = 0$. Then the equality conditions can be used to eliminate λ and obtain

$$\frac{\mu(M)}{\mu(F)} = \frac{c_F}{c_M} \quad \text{or} \quad \frac{c_M \mu(M)}{c_F \mu(F)} = 1 \tag{96}$$

The first version states that the sex ratio in numbers is the ratio of costs, and the second that the sex ratio in investment is equal.

This is one of the most famous arguments in evolutionary biology, and there have been many formal and informal versions with the same conclusion. The arguments are reviewed by Edwards (1998) and Seger & Stubblefield (2002), and see also Edwards (2000) for a fascinating historical discovery. Most authors have made only informal links between reproductive value methods and rigorous population genetics in sex ratio arguments, and Seger & Stubblefield (2002) present them as

distinct and complementary. However, the two approaches were explicitly and formally bridged by Taylor (1996, uncited by Seger and Stubblefield), who therefore provided the first rigorous version of the reproductive value argument. The present paper extends this by permitting a further class structure within each of the sexes, which we proceed to exploit.

One more sex ratio model needs to be mentioned here. Leimar (1996) presented a formal version of the verbal model of Trivers & Willard (1973), and solved in that case many of the technical problems being encountered here. The Trivers-Willard model is perhaps the most prominent evolutionary idea which requires such a careful handling of reproductive value, and Leimar's work shows the importance of taking the formal approach.

8.1.2. An extension

Now suppose class is the Cartesian product of $\{M, F\}$ and $[a, b]$, with $0 < a < b$, and that the population of females on $[a, b]$ is represented by the finite measure ϕ_f and of males by the finite measure ϕ_m. We first discuss the monomorphic population against which mutants will be tested. Suppose females choose the sex of their offspring and all make the same relative distribution of classes within each sex, which must therefore be proportional to ϕ_f and ϕ_m, but may vary in their magnitudes. We will come back to the question of whether it might be advantageous for females of different classes to make different relative distributions. We also assume that females are constrained in offspring production measures g_f and g_m by their own parental class x such that

$$\int y g_f(dy) + \int y g_m(dy) \leq Kx \tag{97}$$

so that it costs y to make an individual of class y, and class is advantageous to a female in allowing her to make more offspring. Suppose that male classes mate independently with female classes, and that the mating success of males in class y is proportional to y^2. Then as individuals of each sex make offspring in sex-specific proportions across the classes, but differ only in the absolute numbers, we can straight away define the invariant measure $\tau = \tau_f + \tau_m$ in its two components for females and males, respectively, by

$$\tau_f(A) = \frac{1}{2} \frac{\int_A y \phi_f(dy)}{\int y \phi_f(dy)} \qquad \tau_m(A) = \frac{1}{2} \frac{\int_A y^2 \phi_m(dy)}{\int y^2 \phi_m(dy)} \tag{98}$$

and the per-capita reproductive values by

$$h_f(y) = \frac{1}{2} \frac{y}{\int y \phi_f(dy)} \qquad h_m(y) = \frac{1}{2} \frac{y^2}{\int y^2 \phi_m(dy)} \tag{99}$$

The evolutionary maximand is therefore incarnated, neglecting for convenience the fixed factor of $\frac{1}{2}$, as

$$\frac{\int y g_f(dy)}{\int y \phi_f(dy)} + \frac{\int y^2 g_m(dy)}{\int y^2 \phi_m(dy)} \tag{100}$$

with the constraint for an individual female in class x represented by equation (97).

We now employ the result (80), in whose terms for the males, we have $f(x) = y^2 / \int y^2 \phi_m(dy)$ and $g(x) = y$. The ratio $f(x)/g(x)$ is therefore $y / \int y^2 \phi_m(dy)$. As y is positive, only the highest value of y can attain a maximum, and so if males are made at all in the optimal solution, then we must have g_m place all its measure on $y = b$, so that the value of λ is $b/(b^2\phi(\{b\})$ which equals $1/(b\phi(\{b\})$. The female ratio is $1/(\int y^2 \phi_f(dy))$ and thus independent of y, so either all female classes or no female classes may be produced at the optimum. We are interested in values of ϕ_f and ϕ_m that might be optimal, so we require that both females and males are made. Thus the ratio for females must equal the ratio for the only permitted male class, showing that

$$\int y\phi_f(dy) = b\phi_m(\{b\}) \tag{101}$$

These terms are respectively the total investment in female and male offspring, and so we have established from first principles Fisher's equal investment result in this context. It is a necessary and sufficient condition for optimality that only b-males be produced and that the investment in both sexes be equal.

This implies that the ratio of different classes as shown in the relative values of ϕ_f is irrelevant to female reproductive value, so ϕ_f may contain atoms and gaps. The optimisation result shows there is no selection to deviate from the given allocation by females to different classes. This is not surprising, as the only advantage to a class for females is its ability to invest, and that ability is proportional to the investment in it. Thus there are equal per-investment returns and the size of the unit is immaterial. This answers in the negative the question posed earlier of whether it might be advantageous for females in different classes to choose a different distribution of offspring. (This does leave open the possibility that if females were polymorphic for ϕ_f, there would be a different outcome of selection, but we neglect that here.)

This treatment of a sex ratio problem has illustrated how Fisher's argument can be extended using the formalism developed in the paper. We have both indifference between investment classes for the females, and an atom showing all males are produced into the same class. These are useful kinds of outcomes to be able to handle.

The tools used here might well with mild extensions allow the development of a complete justification of the reproductive value approach to sex ratio problems frequently used in biology, and as formalised for example by Boomsma & Grafen (1991).

8.2. Rank order for resources, and a non-compact X

We now turn to a parental investment model, in which an amount x is invested to place an offspring in class $x \in [a, \infty)$ with $a > 0$. Resources among the offspring are awarded on a competitive basis, such that only the rank of the offspring by class matters. Specifically, per-capita resources for class x, $r(x)$, are determined so that

$$\int_x^\infty r(x')m(dx') = \sqrt{\int_x^\infty m(dx')} \tag{102}$$

where the total resources are therefore 1. We differentiate with respect to x to obtain

$$r(x) = 1/(2\sqrt{m(\{[x, \infty)\})}) \tag{103}$$

The minimum per-capita resource is therefore $\frac{1}{2}$ for the lowest class, but it rises to ∞ for the highest class.

Consider an individual in class x who has resources $r(x)$ and produces a measure g across offspring classes, and so is subject to the constraint $\int yg(dy) \leq r(x)$. As the maximand and constraint are proportional, it is clear that the per-capita reproductive value must be proportional to $r(x)$ so the invariant measure τ will satisfy $\tau(dx)/m(dx) = \kappa r(x)$ for some $\kappa > 0$. Thus we can write the maximand as $\int r(y)g(dy)$, and the program is

$$g \quad \max \int r(y)g(dy),$$
$$\int yg(dy) \leq K \tag{104}$$

It follows from result (80) that for classes y produced in an optimal solution, we must have $\lambda = r(y)/y$. Standard arguments (e.g. Bishop & Cannings, 1978) show gaps cannot be optimal if they have an upper bound (the same resources are available at a lower cost), and the infinite per-capita resource shows that the support of an optimal solution cannot have an upper bound. Thus we find the population measure that ensures $\lambda = r(y)/y$ for the whole interval $[a, \infty)$, which is

$$m(dy) = \frac{2a^2}{y^3}dy \tag{105}$$

The space of classes X is not compact, but nevertheless, the existence of τ is not in doubt in this example. However, a further result of Rosenblatt (1971, page 104), beyond that discussed in Section 4.3, is worth mentioning in this context for a measure space based on a metric space X, its Borel sets $\mathfrak{X}$ and a measure μ. In place of compact X, and T taking continuous functions to continuous functions, we may instead have locally compact X, and T taking bounded continuous functions to bounded continuous functions. An additional requirement is that there is a compact subset of X through which the trajectory of each point $x \in X$ passes with probability one. Then the theorem tells us that there exists an invariant measure which is sigma-finite. This means there is an at most countable subset of $\mathfrak{X}$ whose union covers X, and over each element of which the measure is finite.

The condition of trajectories passing through a compact subset refers to a trajectory of ancestors in the biological case. It states that there must be a compact set such that for every individual lying outside that set, the probability that their ancestral path at no point intersects the compact set is zero. In this example, each individual has an equal finite chance that its immediate ancestor lies in $[a, a + 1]$, so the probability that at least one ancestor lies in $[a, a + 1]$ is indeed one.

8.3. A geographical example

Suppose X represents geographical space, which may be a compact subset in one, two or three-dimensional space, that μ represents the Borel measure, and that there is another measure p over X representing the rate at which a region can produce offspring. The total productivity of a region A is fixed by $p(A)$, and shared among the $\mu_X(A)$ individuals present there. The offspring produced may be distributed in space, and we suppose that the common strategy is represented by a function $s(x, y)$ which equals 1 if parents at x produce offspring at y, and 0 otherwise. We define sets of the parents that produce given offspring and the offspring produced by given parents as follows:

$$P(y) = \{z \colon s(z, y) = 1\} \qquad O(x) = \{z \colon s(x, z) = 1\} \tag{106}$$

We make two further assumptions about reproduction. We assume that parents at x produce offspring evenly over $O(x)$, and that offspring are spread over a region whose Borel measure (area in two dimensions) is a constant β^{-1} for all parents. Thus

$$v(x)(dy) = \begin{cases} \beta \frac{p(dx)}{\mu_X(dx)} \mu(dy) & y \in O(x) \\ 0 & y \notin O(x) \end{cases} \tag{107}$$

$$\beta^{-1} = \mu(O(x)) = \int s(x, y)\mu(dy) > 0 \tag{108}$$

This allows us to write $(Tf)(y)$ as

$$(Tf)(y) = (\mathbb{D}_V \, \mathbb{E}\,[f v])\,(y) = \beta \frac{\int_{P(y)} f(x)p(dx)}{\int_{P(y)} p(dx)} \tag{109}$$

If the population reaches an equilibrium of class dynamics, then as each parent produces a density there can be no atoms of population. We proceed on the basis that there exists a function h representing the per-capita reproductive value of offspring. We aim to find the optimisation program based on the choices of a particular individual. Let $e(y)$ be the indicator function of the set of locations within which that individual is free to place offspring, and let the strategy function be f. We can represent the program as

$$f \quad \max \quad \int e(y)f(y)h(y)dy,$$
$$\int f(y)dy \le K$$
$$f(x) \le 1$$
$$f(x) \ge 0 \tag{110}$$

This program can be solved using result (82). Thus an area Q with the highest values of $e(y)h(y)$ is fully occupied, and an area R with the unique marginal value c^* of $e(y)h(y)$ is occupied to the extent required to 'use up' the area an individual can place offspring into.

If $e(y)$ is uniformly 1, so there are no restrictions on where individuals can place offspring, then this shows that the area of 'super-normal profits' is small enough to be less than the area of one individual's offspring. This provides what is very close to an 'ideal free distribution' (Fretwell, 1972), in which the distribution of organisms matches the distribution of resources, and the per-capita reproductive values are equal. There is only a small exceptional area caused by the restriction that individuals cannot fully concentrate their offspring.

If $e(y)$ differs between individuals, perhaps so that individuals can place off-spring only near to their own location, then the whole argument would become more complicated as the value of c^* could vary from place to place. This example has shown how the reproductive value methods developed in this paper can in outline be applied to geographical questions.

9. Comparison with Taylor

Taylor (1990) provided a theory of reproductive value for finite X. Here a comparison is made between Taylor's theory and that of the current paper. There is one important difference in emphasis. Taylor does not particularly link his results to the work of Fisher (1930), whereas the whole of Section 7 shows how the results provide a formal justification of an underlying structure in Fisher's evolutionary analyses.

The formal differences will be discussed using the notation of the present paper. The first difference is that Taylor's X is finite while here it is compact Hausdorff, which implies it can have continuous and discrete components and can be multi-dimensional. One advantage of this generality is that some examples, such as parental care or location, might be more naturally modelled with continuous components. Even some infinite-dimensional sets could be handled, perhaps representing shape. Another advantage is that reproductive value is shown in a wider context to play an essential role in natural selection.

The second difference is that Taylor assumes a very simple diploid genetics, with a single locus with two alleles, one of which is a rare mutant; and restricts attention to a one-dimensional space of phenotypes. Here initially a general genetics is permitted with arbitrary ploidy, in which the change in an arbitrary p-score is discussed, and the set of phenotypes is arbitrary. This allows multiple alleles at multiple loci, and arbitrary epistasis and linkage. The main Price equation derived by Taylor has the same form as here, in being an average over classes of a covariance within each class, but his equation (16) holds only to second order in the mutant frequency, while here the main Price equation (equations 22 and 23) is exact in expectation with arbitrary genetics. For some parts, notably Section 6 in discussing equilibrium, the present paper does move much closer to Taylor, assuming genetic uniformity apart from a rare mutant, and restricting attention to just two phenotypes.

Taylor does not discuss the ambivalence of equilibrium concepts discussed in Section 6, as he considers only the reproductive-value-weighted gene-frequency as indicating success of an allele. In the 1990 paper, he permits the rare mutant to have an arbitrary phenotype, and states his results to first order in the mutant frequency. This position neglects the possibility that the new phenotype might alter

its own class distribution so that the reproductive-value-weighted gene-frequency is no longer a good measure of the success of an allele. In our terms, such a strategy might spread under the clonal growth condition but not under the tracer-allele condition. In 1996, Taylor makes the additional assumption that the mutant phenotype is very close to the common phenotype, and so resolves this difficulty.

Taylor (1996) does however have a different distinction to draw, between mutant stability (whether a fixed population is stable against a small population of mutants) and population stability (whether a population slightly displaced as a whole from an equilibrium induces selection pressures that tend to restore the original state). From a formal point of view, even the definition of population stability is phrased in terms of a very simple strategy set, namely the real line, and for that reason does not fit in to the level of generality of the present paper. On the other hand, the Price equation (in equations 22 and 23) applies to situations of genetic variability, and so has information about out-of-equilibrium behaviour.

Taylor's finite X means he has no problems with existence of reproductive values, which here has Section 4.4 devoted to it, but neither does he discuss uniqueness. Here, the issue of uniqueness is given a biological interpretation in Section 5.

Taylor analyses the forwards process of changing gene frequencies as well as the backwards process of reproductive value, and obtains very appealing results. See Taylor (1990, page 98–99) and Taylor (1996, page 664). Here, I bring together the analogous results in the present paper. The left and right eigenvectors of Taylor's forward process are represented here by the eigenvectors of $\tilde{T}$ and $\tilde{U}$, respectively, and satisfy

$$\lambda h = \tilde{T} h \qquad\qquad \lambda \mu_X = \tilde{U} \mu_X \qquad\qquad (111)$$

$$\lambda h(x) = \int h(y) v(x)(dy) \quad \lambda \mu_X = \int v(x) \mu_X(dx) \qquad (112)$$

Existence is discussed in Section 4, but where they do exist, h gives the per-capita reproductive value of each class, and μ_X is the equilibrium population distribution over classes.

The results for the backwards process, including the left and right eigenvectors, are more complicated to express in terms of v. We assume an equilibrium of class dynamics so that μ_X is an eigenvector of $\tilde{U}$ and $\tilde{U} \mu_X = V = \lambda \mu_X$. We will use f_A to represent the indicator function of a set A. The left eigenvector is a measure representing the class reproductive values, and the right eigenvector is the function always taking the value 1, which will be written f_X. These results derive from the definitions of the Markov process in Section 3.1:

$$\tau(A) = \int P(y, A) \tau(dy) \qquad f_X(x) = \int f_X(y) P(x, dy) \qquad (113)$$

$$\tau(A) = \int (\mathbb{D}_V \, \mathbb{E}\,[f_A v])(x) \tau(dx) \;\; f_X = \mathbb{D}_V \, \mathbb{E}\,[f_X v] \qquad (114)$$

A major extra feature in Taylor's analysis is that he allows social interactions, and states inclusive fitness results. Interestingly, one main point seems to be to discuss an individual optimisation framework: the simpler example of Fisher's

Fundamental Theorem was not taken seriously at the time. Taylor's 1990 appendix is the only serious elaboration of the somewhat cryptic argument of Hamilton (1970, in which inclusive fitness is derived from the Price equation for the first time), but is only fully presented for an example. The complete inclusive fitness result in the present framework is beyond the scope of this paper, but the formal Darwinism project is extended to inclusive fitness by Grafen (2006).

Thus the present paper is in some ways an advance on Taylor and in others lags behind, but the general thrust of justifying and defining reproductive value is fully shared. The most unfortunate relationship lies in notation. As he has a finite number of classes, Taylor worked with matrices and it was natural to use i to index the classes; then to index individuals, he used x and y. It is, however, more conventional in work on the Price equation to use i to index the individuals; and the more abstract nature here made it natural to use X for the space of classes and so x and y for elements of that set, namely for classes themselves. Thus for understandable reasons, Taylor writes the number of class i offspring of individual x as w_{ix}, while here I would write the number of class x offspring of individual i (with a differential element because $w(i)$ is a measure) as $w(i)(dx)$. This conflict of notation should not disguise the commonality of intent.

10. Conclusions

Fisher's uses of reproductive value are illuminated and explained by a combination of the Price equation, and the theories of Markov processes and positive operators. A wide range of kinds of biological classes are shown to support reproductive values. The formal mathematics shows how generally the concept of reproductive value applies in biology, and also provides a framework within which particular problems can be worked out.

The main conclusion from the paper is that adaptive arguments along the lines of Fisher's sex ratio argument, in which the organism is viewed as an optimising agent, can be made fully rigorous in population genetic terms in the presence of classes. It also extends the Price equation to allow classes.

With the advance of molecular genetics and bioinformatics, more disciplines are encountering questions about the operation of natural selection. Population geneticists have a mathematically rigorous tradition and are already prepared, but there are other important areas of Darwinian biology, notably those relying (sometimes implicitly) on optimisation principles. To make the accumulated understanding of Darwinian biologists available to other disciplines, it must be translated into the universal scientific language of mathematics.

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