$$\iota^{**}=7/3\psi$$

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Two contrasting interpretations of Fisher's fundamental theorem of natural selection

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Abstract The modern interpretation of Fisher's fundamental theorem of natural selection is based on Price (1972, *Ann. Hum. Genet., Lond.,* 36:129–140). Like Fisher he described the theorem as a balance between a partial increase in fitness caused by natural selection and a partial decline caused by the deterioration of the environment. But to obtain generality Price sacrificed fitness as a phenotypic trait with a well-defined genetic and environmental component. This contrast with a more resent phenotypic interpretation (Witting, 2000, *Acta Biotheor.,* 48:107–120) where fitness is treated as a well-defined phenotypic character. The two interpretations are compared and it is discussed that the generality of the modern interpretation may be in conflict with Fisher. As predicted by the phenotypic interpretation, Fisher described the fundamental theorem as if it applies only to an ecological vacuum where there are no interactions among individuals.

Keywords: Natural selection, exploitative competition, interference competition, density regulation, life-history evolution

1 Introduction

When Fisher (1930) introduced the fundamental theorem of natural selection he defined fitness as the Malthusian parameter that "measures fitness by the objective fact of representation in future generations". This parameter is calculated from the rates of reproduction and mortality so that fitness is a phenotypic trait that reflects the joint expression of a genetic and an environmental component. But in nearly all discussions of the fundamental theorem the treatment of fitness as a phenotypic trait has remained implicit and vague.

In this paper I compare two alternative interpretations that aim at a better understanding of the fundamental theorem by decomposing fitness into underlying components. The first was introduced by Price (1972a) and it is now referred to as the *modern interpretation* (Frank 1995). Here the change in fitness is partitioned into apparent "natural selection" and "environmental" components in order to obtain a correct mathematical statement that holds in nearly all cases. As noted already by Price (1972a), this framework does not solve the problem of treating fitness as a fixed standard where the phenotypic expression can be partitioned into underlying genetic and environmental components. This is because the components of natural selection and environment in the modern interpretation do not strictly correspond with the genetic and environmental components of the phenotypic character fitness.

The fitness decomposition of the modern interpretation is to some extend in contrast with Fisher's (1930) own treatment of fitness in relation to the fundamental theorem. On several occasions in "The Genetical Theory of Natural Selection" Fisher discusses fitness as if the genetic component is the *intrinsic* Malthusian parameter, where a natural selection increase in this parameter results in an increase in the population dynamic equilibrium. This *phenotypic interpretation* was analysed by Witting (2000a) who described the fundamental theorem by partitioning fitness changes into changes in the underlying genetic and environmental components, with the genetic changes being the direct response to natural selection. Interestingly this hypothesis reconciles statements by Fisher that are left unexplained by the modern interpretation. But the phenotypic interpretation also suggests that the fundamental theorem applies only to an ecological vacuum where there are no interactions among individuals.

1.1 The fundamental theorem of natural selection

Having defined fitness as the Malthusian parameter Fisher (1930) introduced the fundamental theorem as

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

Not realising that this increase relates only to a partial increase caused by natural selection, there soon grew the misinterpretation that the theorem deals with an overall increase in the average Malthusian parameter

of the population (e.g., Wright 1930, 1955; Li 1955; Kempthorne 1957; Crow and Kimura 1956; Kimura 1958, 1965; Kojima and Kelleher 1960; Ewens 1969). And as it is evident that the rate of population dynamic increase does not generally increase, the theorem was soon seen as an exception that applies only to special cases like an unchecked population in a density independent environment.

But as pointed out by Price (1972a), a closer reading of Fisher (1930) indicates that the increase in fitness is only a partial increase caused by natural selection. For example, on page 42, in the "Complete Variorum Edition" (Fisher 1999), Fisher states that

> The balance left over when from the rate of increase in the mean value of m produced by Natural Selection, is deducted the rate of decrease due to deterioration in the environment, results not in an increase in the average value of m, for this average value cannot greatly exceed zero, but principally in a steady increase in population.

Here the increase in fitness is treated as an implicit increase in the intrinsic Malthusian parameter (Witting 2000a), and there is thus no doubt that Fisher realised that the average Malthusian parameter cannot generally increase. But under what general conditions will natural selection cause the intrinsic Malthusian parameter to increase? This question was not addressed by Fisher and nor by the modern interpretation of the fundamental theorem. In Sections 2 and 3 I examine the degree to which this question can be addressed within the frameworks of respectively the modern and the phenotypic interpretations.

2   The modern interpretation

Price (1972a) aimed at a formal deduction of the fundamental theorem by partitioning fitness into an environmental and natural selection component. Like Fisher he argued that the overall change in fitness (Δr) is best understood in terms of a partial increase caused by natural selection (Δr_{ns}) and a partial decline caused by the deterioration of the environment (Δr_{ec}). In consequence

$$\Delta r = \Delta r_{ns} + \Delta r_{ec} \qquad (1)$$

The fitness in two subsequent generations were then defined as

$$r = \sum_{l,k} b_{r,lk}\, p_{lk} \qquad (2)$$

$$\acute{r} = \sum_{l,k} \acute{b}_{r,lk}\, \acute{p}_{lk}$$

where l denotes a gene locus, k a particular allele of locus l, p_{lk} and $\acute{p}_{lk}$ the population frequency of allele k at locus l in the two generations, and $b_{r,lk}$ and $\acute{b}_{r,lk}$ the partial linear regression of the Malthusian parameter r on the allele lk frequency in the population in those generations. Thus, from eqn 2, the change in the Malthusian parameter is

$$\Delta r = \acute{r} - r = \sum_{l,k} \acute{b}_{r,lk}\, \acute{p}_{lk} - \sum_{l,k} b_{r,lk}\, p_{lk} \qquad (3)$$

The partial changes caused by natural selection and the deterioration of the environment were then defined as

$$\Delta r_{ns} = \sum_{l,k} b_{r,lk}\, \acute{p}_{lk} - \sum_{l,k} b_{r,lk}\, p_{lk} \qquad (4)$$

$$\Delta r_{ec} = \sum_{l,k} \acute{b}_{r,lk}\, \acute{p}_{lk} - \sum_{l,k} b_{r,lk}\, \acute{p}_{lk} \qquad (5)$$

By adding eqns 4 and 5, as indicated by eqn 1, we obtain the overall fitness change of eqn 3. Price then deduced the fundamental theorem by showing that eqn 4 is also the additive genetic variance in r.

Although both Fisher (1930) and Price (1972) argue that it is the increase of natural selection and the environmental deterioration that give the total change in fitness, at the end of his paper Price noted that the theorem apparently fails in defining fitness as some fixed standard. This was mentioned also by Ewens (1989) who argues that there may be no justification for singling out the partial changes caused by respectively the environment and natural selection. The problem with the modern interpretation is that the regression coefficients $b_{r,lk}$ are recalculated in each generation. This implies that even though eqn 4 represents the change in the additive genetic variation caused by natural selection this change cannot be added over time because the changes of subsequent versions of eqn 4 do not have a fixed point of reference. The recalculation of the regression coefficients $b_{r,lk}$ implies that some of the natural selection changes in the additive genetic variation can be transferred into the component of the environmental deterioration. In turn this gives the paradox that the component that is defined to track the additive genetic changes that are caused by natural selection is no more involved in the additive genetic changes than are the environmental deterioration that is defined to exclude the additive genetic changes.

3 The phenotypic interpretation

In order to avoid the paradox that the environmental component of fitness is also representing the genetic component and vice versa, it is essential that the additive genetic change in fitness is defined as a fixed intrinsic component that is mutually exclusive from the environmental component. It is only if we take this consequence of the phenotypic character fitness that we will be able to understand fitness as a fixed standard and to investigate in more detail why and under what conditions fitness is actually increasing.

An initial examination of the phenotypic interpretation of the fundamental theorem was performed by Witting (2000a). Being interested in the ecological component he examined a relatively simple hereditary model with asexual reproduction and additive genetic variation. For the case with exploitative competition and no interactions among individuals the average Malthusian parameter at the population dynamic equilibrium ($*$) were given as

$$r^* = \tilde{r} + \epsilon^* = 0 \qquad (6)$$

where $\tilde{r}$ is the average intrinsic (genetic) Malthusian parameter and ϵ^* the environmental component at population dynamic equilibrium. By summing over the genetic variants in the population these two terms are defined as

$$
\begin{aligned}
\tilde{r} &= \sum_i \tilde{r}_i \, p_i \qquad (7) \\
\epsilon^* &= \epsilon^* \sum_i p_i
\end{aligned}
$$

where p_i is the frequency of the ith variant, and the environmental component is identical to all variants because it is assumed here that there is exploitative competition where all individuals have equal access to the resource.

The partial change in r^* caused by natural selection can then be denoted by $\partial_{ns} r^*/\partial t$ and the partial change in the environment $\partial_{ec} r^*/\partial t$. From eqn 6 it is apparent that $\partial_{ns} r^*/\partial t$ is equivalent to the evolutionary changes in the intrinsic Malthusian parameter $d\tilde{r}/dt$, i.e.,

$$\partial_{ns} r^*/\partial t = d\tilde{r}/dt \qquad (8)$$

And as $dr^*/dt = 0$ by eqn 6 we have that the partial change in the environment is

$$\partial_{ec} r^*/\partial t = d\epsilon^*/dt = -d\tilde{r}/dt \qquad (9)$$

In this case we may use the secondary theorem of natural selection (Robertson 1968) to show that the increase ascribable to natural selection is equal to the additive genetic variance. This theorem states that the change in a trait like $\tilde{r}$ caused by natural selection is

$$d\tilde{r}/dt = \dot{\tilde{r}}\sigma^2 \qquad (10)$$

where σ^2 is the additive genetic variance in $\tilde{r}$ and $\dot{\tilde{r}}$ is the selection gradient

$$\dot{\tilde{r}} = \partial r_i^*/\partial \tilde{r}_i|_{\tilde{r}_i = \tilde{r}} = 1 \qquad (11)$$

Hence, from eqns 8, 10, and 11 we obtain the fundamental theorem

$$d\tilde{r}/dt = \partial_{ns} r^*/\partial t = \sigma^2 \qquad (12)$$

As this increase in the intrinsic Malthusian parameter results not in an increase in r^* but in an increasing equilibrium abundance (Witting 2000a), the phenotypic interpretation with exploitative competition is consistent with Fisher's own statement that natural selection results "in a steady increase in population".

3.1 The limit of interactive competition

But the increase in population envisioned by Fisher is applicable only for the case with exploitative competition and no interactions among individuals. For the case with competitive interactions the resource is unevenly distributed over the individuals in the population so that the average environmental component at population dynamic equilibrium is

$$\epsilon^* = \epsilon^* + \sum_i \Delta\epsilon_i^* p_i \qquad (13)$$

where $\Delta\epsilon_i^*$ is the deviation in the environmental component of the ith variant from the population average. And as the intrinsic Malthusian parameter is related to the individual's interactive quality by an energetic trade-off, with a linear approximation the deviation in the environmental component is

$$\Delta\epsilon_i^* = \psi\iota^*(\tilde{r} - \tilde{r}_i) \qquad (14)$$

where ι^* is the level of interactive competition in the population and ψ represents the slope of the environmental component to the intrinsic Malthusian parameter at the equilibrium level of interactive competition. In this case the selection gradient on the intrinsic Malthusian parameter is

$$\dot{\tilde{r}} = \partial r_i^*/\partial \tilde{r}_i|_{\tilde{r}_i = \tilde{r}} = 1 - \psi\iota^* \qquad (15)$$

and, thus, the change in the intrinsic Malthusian parameter caused by natural selection is

$$d\tilde{r}/dt = \partial_{ns} r^*/\partial t = (1 - \psi\iota^*)\sigma^2 \qquad (16)$$

This change is generally less than predicted by the fundamental theorem [eqn 12]. And for population dynamic equilibria above the evolutionary equilibrium where $\iota^* = 1/\psi$ there is a decline both in the intrinsic Malthusian parameter and in the population dynamic equilibrium.

4   Discussion

Although it will probably never be revealed, it is intriguing whether Fisher was thinking in terms of exploitative competition and exact genetic and environmental components when he defined the fundamental theorem, or whether he was thinking in more general ecological settings and unspecified genetic and environmental components. The history of evolutionary biology in general, where at that time it was the custom to think in terms of constant relative fitnesses, and the population genetical focus of Fisher in particular, where ecological interactions can be seen as a distant disturbing dimension, point in the direction of the phenotypic interpretation with exploitative competition. This may also be the only case where there is no contradiction in Fisher's treatment of the fundamental theorem. In particular, Fisher's discussions of an increase in the abundance caused by the balance between the increase of natural selection and the deterioration of the environment is in direct contradiction with the ecology of interactive competition.

The advantage of the modern interpretation is its generality and potential of being integrated into larger frameworks. In consequence, the fundamental theorem is now generally regarded as a correct mathematical statement (e.g., Frank and Slatkin 1992; Edwards 1994; Burt 1995), and it has now become deeply integrated in the framework of population genetics (Castilloux and Lessard 1995; Lessard and Castilloux 1995; Frank 1997, 1998; Lessard 1997; Yi and Lessard 2000). Nevertheless, the modern interpretation sets limits to our understanding of fitness in terms of the traits that are selected for by natural selection. In order to understand fitness in more detail we need to treat fitness as a phenotypic character that is defined from genetic and environmental components realising that their joint expression is often dependent upon complex interactions at levels at and beyond the individual organism. This approach has proven successful by showing that the intrinsic Malthusian parameter can reflect fitness for the case of exploitative competition, while fitness can be seen as a density and frequency dependent balance between the intrinsic Malthusian parameter and interactive quality for the alternative case with density dependent competitive interactions (Witting 2000a).

This conclusion is also reflected by a parallel development in the theory of life history evolution. The exploitative case of the phenotypic interpretation of the fundamental theorem resembles r and k selection, where the partial increase in the intrinsic Malthusian parameter generates an increase in the population dynamic growth rate (r) or in the carrying capacity (k). Usually it is agreed that r and k selection was developed conceptually by MacArthur (1962) and MacArthur and Wilson (1967), and that the mathematical theory was constructed by Anderson (1971), Charlesworth (1971, 1980, 1994), Roughgarden (1971) and Clarke (1972). But as described here it seems that Fisher may have been the first to consider selection on the continuum from r to k.

The optimisation of r and k selection underlies most of the classical life history models that are reviewed by Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994). But recently the trend in life history theory has been toward the more elaborate selection principles of Evolutionary Stable Strategies (Maynard Smith and Price 1973), Continuously Stable Strategies (Eshel and Motro 1981), and Evolutionary Branching (Metz et al. 1996) all of which allow for interacting individuals.

Under Fisher's interpretation that the increase of natural selection results "in a steady increase in population", the fundamental theorem cannot be a general principle because this is generally true only in the absence of interactions among individual organisms. Thus, from eqn 16, it is suggested that the theorem may apply to natural populations only as a limit at zero population density where $\iota = 0$ and there are no interacting individuals. If, at this limit, the additive genetic variance is constant, the fundamental theorem gives an exponential increase in the Malthusian parameter

$$dr/dt = \sigma^2 \qquad (17)$$

Then, by solving eqn 17 and $dN/dt = rN$ we find that the population abundance will increases hyper-exponentially as

$$N_t = N_0 e^{r_0 t + \sigma^2 t^2/2} \qquad (18)$$

where N_0 and r_0 are respectively the abundance and Malthusian parameter at time $t = 0$. This increase reduces into the Malthusian law (Malthus 1798) of exponential increase

$$N_t = N_0 e^{rt} \qquad (19)$$

at the limit $\sigma^2 = 0$ with no additive genetic variance. This degree of change in population dynamics caused

by natural selection may apply not only at zero population density. When, at larger densities, selection by competitive interactions are incorporated into population dynamics we can expect cyclic dynamics instead of the monotonic return to equilibrium that tends to be predicted by traditional density regulated models (Witting 2000b).

The indication that the fundamental theorem may apply only as a limit at zero population density, however, is based on the implicit assumption that the genetic component of fitness is the intrinsic Malthusian parameter. As already discussed this is generally not the case. So if we could identify the true genetic component to fitness it might be that a new interpretation of the fundamental theorem could hold as a general principle. If so it is somewhat ironic that the direction of natural selection changes in the Malthusian parameter is more likely toward a decline instead of the increase envisioned by Fisher (Witting 1997, 2002).

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