$\iota^{**}{=}7/3\psi$
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Interference competition set limits to the fundamental theorem of natural selection

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Abstract The relationship between Fisher's fundamental theorem of natural selection and the ecological environment of density regulation is examined. Using a linear model, it is shown that the theorem holds when density regulation is caused by exploitative competition, and that the theorem fails with interference competition. In the latter case the theorem holds only at the limit of zero population density and/or at the limit where the competitively superior individuals cannot monopolise the resource. The results are discussed in relation to population dynamics and life history evolution, where evidence suggests that the level of interference competition in natural populations is so high that the fundamental theorem does not apply.

1 Introduction

Fisher's fundamental theorem of natural selection (Fisher 1930) suggests that natural selection causes a partial increase in the average Malthusian parameter (r) of a population, and that the population evolves toward an equilibrium where the partial increase is balanced against a partial decline caused by the populations impair of the environment. The result is an average Malthusian parameter that takes a rather stable value around zero while the population equilibrium, or carrying capacity, increases steadily. This paper deals with the partial increase in r caused by natural selection. It examines a limit to the predicted increase caused by density dependent interference competition, and it discusses the implications that the limit has for population dynamics and life history evolution.

Fisher considered the fundamental theorem to be of great importance. But the importance remained obscure until Price (1972a) made a formal deduction indicating that the theorem holds for all cases. From Fisher's formulation there had grown the misinterpretation that the fundamental theorem dealt with the overall increase in the average Malthusian parameter of a population (e.g., Wright 1930, 1955; Li 1955; Kempthorne 1957; Crow and Kimura 1956; Kimura 1958, 1965; Kojima and Kelleher 1960; Ewens 1969). Consequently, the theorem was seen as a special case

that failed for most natural populations (see Kimura 1958; Li 1967; Karlin and Feldman 1970; Turner 1970; Elandt-Johnson 1971; Jacquard 1974; reviewed Edwards 1994). But Price (1972a) made it clear that the fundamental theorem makes statements only about a partial increase caused by natural selection, and since Price the theorem has regained its glory as a correct mathematical statement (e.g., Frank and Slatkin 1992; Edwards 1994; Burt 1995).

To understand the fundamental theorem it is essential to treat genotypic components like dominance and epistasis as part of the environment. Adopting this somewhat unusual point of view the analyses of Price (1972a) and Ewens (1989, 1992) suggest that the theorem hold as a general principle. Recent theoretical work by Lessard and Castilloux (Castilloux and Lessard 1995; Lessard and Castilloux 1995; Lessard 1997) have increased the integration between the fundamental theorem and the framework of population genetics, and Frank (1997, 1998) has used the Price Equation (Price 1970, 1972b) as a general basis for a unification of diverse disciplines like the fundamental theorem, Robertson's covariance theorem for quantitative genetics (Robertson 1966), and Hamilton's rule for kin selection (Hamilton 1964).

The fundamental theorem is a major cornerstone for classical life history theory. Nearly all the life history models in the books of Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994) are optimality models that define natural selection by an increase in the Malthusian parameter (r) or by an increase in the carrying capacity (k) for populations at population dynamic equilibria. It is usually agreed that this concept of r and k selection was developed by MacArthur (1962) and MacArthur and Wilson (1967), and elaborated into a mathematical theory by Anderson (1971), Charlesworth (1971, 1980, 1994), Roughgarden (1971) and Clarke (1972). However, the theoretical distinction between r and k selection was probably first formulated by Fisher (1930) when he proposed the fundamental theorem.

Fisher defined fitness as the Malthusian parameter, usually denoted r, but denoted m by Fisher. This parameter is the solution to the Euler equation and it "measures fitness by the objective fact of representation in future generations" (Fisher, 1958 p. 37). The fundamental theorem deals with a partial increase in fitness, but as explained by Price (1970), Fisher's first definition of the theorem (Fisher 1930) was unclear because it did not specify what Fisher meant with the term *increase in fitness*. This was specified in 1941:

> the rate of increase in the average value of the Malthusian parameter ascribable to natural selection ... is ... equal to the genetic variance of fitness (Fisher, 1941:57)

As pointed out by Price (1972a), the term "ascribable to natural selection" indicates that the increase in r is a partial increase and that the total change contains also other parts. In "The Genetical Theory of Natural Selection" Fisher discussed these remaining parts in the light of density regulation, and he concluded 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. (Fisher, 1958:45-46)

In other words, apart from the partial increase in r (m) caused by natural selection, there is a partial decline in r caused by density regulation, and for populations in population dynamic equilibrium the two partial rates have the same absolute value so that the total change in r is zero, while the carrying capacity increases steadily. Hence, dependent upon the density dependent situation, natural selection can be understood either in terms of a partial increase in r and/or in terms of a continuous increase in k.

This hypothesis of r and k selection is essential for classical life history theory. If natural selection generates a partial decline in r it makes no sense to define natural selection by optimality models that are based on a partial increase in r. Since Prout (1980) and Mueller and Ayala (1981) it has been known that it is not strictly true that natural selection generates an increase in r. Nevertheless, recent work on the fundamental theorem suggests that it holds as a general principle (e.g., Price 1972a; Ewens 1989, 1992; Castilloux and Lessard 1995; Lessard and Castilloux 1995; Frank 1997), and it is often argued that the critique

against the theorem (e.g., Wright 1930, 1955; Li 1955; Kempthorne 1957; Crow and Kimura 1956; Kimura 1958, 1965) fails because the critique deals with a total change in r while Fisher considered only a partial increase. In this paper it is shown that the distinction between a partial and a total change in r does not save Fisher's idea of a partial increase in r. Section 2 shows that a partial increase in r caused by natural selection is expected for the case with exploitative competition, but Section 3 shows that a partial increase is not expected for the case with interference competition. Although these results hold theoretically the fundamental theorem may still apply to natural populations. This would be the case if the selection pressure on the Malthusian parameter in natural populations were determined by exploitative competition. In section 4 it is discussed whether evidence among natural populations favours the hypothesis that the selection pressure on the Malthusian parameter is determined predominantly by exploitative or interference competition.

2   Exploitative competition

In this section it is shown that the fundamental theorem of natural selection holds for the situation with exploitative competition and no interactions among individuals and genotypes. To show this let the average Malthusian parameter (r) among the individuals in a population be defined as

$$r = \tilde{r} + \epsilon \tag{1}$$

where $\tilde{r}$ is the average intrinsic Malthusian parameter, which represents the intrinsic or additive genetic component to the Malthusian parameter, and ϵ is the environmental component that, in accordance with Fisher (1958) and Price (1972a), reflects both the ecological environment and genotypic components like dominance and epistasis. This definition implies that the additive genetic variance in r is equivalent with the additive genetic variance in $\tilde{r}$.

This study deals with limitations to the fundamental theorem imposed by density dependent interference competition and, thus, for simplicity, it can be assumed that the genotypic environment is constant. Density regulation by exploitative competition can then be defined as

$$\epsilon = \hat{\epsilon} - \gamma_\alpha n \tag{2}$$

where $\hat{\epsilon}$ is the environmental component ϵ for individuals on unexploited resources, n is the population density, and γ_α density regulation by exploitative compe-

tition. Hence, combining eqns 1 and 2,

$$r = \tilde{r} + \hat{\epsilon} - \gamma_\alpha n \qquad (3)$$
$$= \hat{r} - \gamma_\alpha n$$

where $\hat{r} = \tilde{r} + \hat{\epsilon}$ is the average Malthusian parameter r for individuals on unexploited resources. The density at the population equilibrium $r^* = 0$ is then $n^* = \hat{r}/\gamma_\alpha$, with star denoting population equilibrium. At equilibrium

$$r^* = \tilde{r} + \epsilon^* = 0 \qquad (4)$$

with $\epsilon^* = \hat{\epsilon} - \gamma_\alpha n^* = -\tilde{r}$ being the environmental conditions at equilibrium.

Following the notation of Price (1972a), the partial change in r^* caused by natural selection can be denoted as $\partial_{ns}r^*/\partial t$, and the partial change in r^* caused by the deterioration of the environment as $\partial_{ec}r^*/\partial t$. Thus, from eqn 4, it is apparent that $\partial_{ns}r^*/\partial t$ is equivalent to the evolutionary change in the intrinsic Malthusian parameter $d\tilde{r}/dt$, i.e.,

$$\partial_{ns}r^*/\partial t = d\tilde{r}/dt \qquad (5)$$

As $dr^*/dt = 0$ by eqn 4, it follows that the partial change in r^* caused by the deterioration of the environment is

$$\partial_{ec}r^*/\partial t = d\epsilon^*/dt = -d\tilde{r}/dt \qquad (6)$$

Equation 1, 3, and 4 describe the average fitness of the population as a function of the intrinsic Malthusian parameter of the average variant in the population. The fitness profile for $\tilde{r}$, on the other hand, describes the fitness of the ith variant in a population as a function of the intrinsic Malthusian parameter of the ith variant. With exploitative competition all variants in a population at population dynamic equilibrium experience the same environmental conditions ϵ^* and, thus, from eqn 4 the fitness of the ith variant is

$$r_i^* = \tilde{r}_i + \epsilon^* \qquad (7)$$

with i denoting the ith variant. The selection gradient on the average intrinsic Malthusian parameter is then

$$\dot{\tilde{r}} = \lim_{\tilde{r}_i \to \tilde{r}} dr_i^*/d\tilde{r}_i = 1 \qquad (8)$$

From the secondary theorem of natural selection (Robertson 1968) the evolutionary change in the intrinsic Malthusian parameter $\tilde{r}$ is

$$d\tilde{r}/dt = \dot{\tilde{r}}\sigma^2 \qquad (9)$$

where σ^2 is the additive genetic variance in $\tilde{r}$ and, thus, also in r^*. Hence, by eqn 8, the intrinsic Malthusian
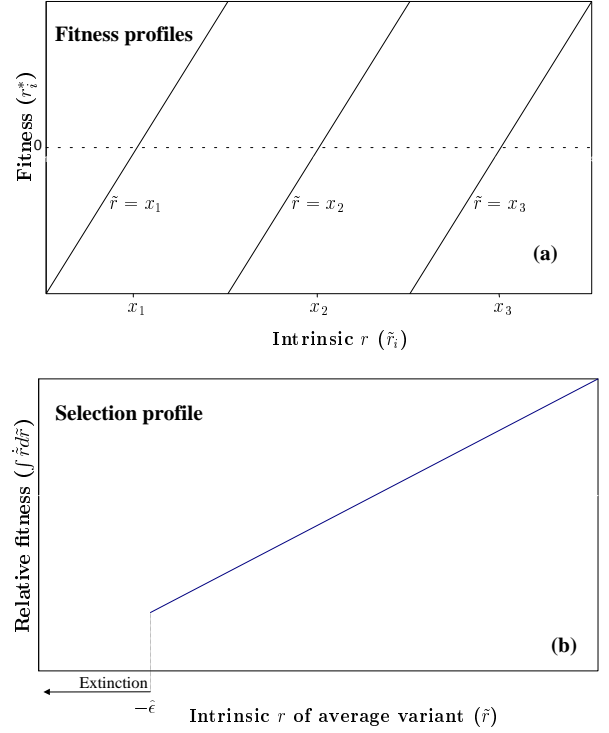

Figure 1: The case with only exploitative competition. **a)** The fitness profile, which describes the fitness of the ith variant in the population (r_i^*) as a function of the intrinsic Malthusian parameter of that variant ($\tilde{r}_i$), for three populations that differ in the average intrinsic Malthusian parameter ($\tilde{r}$). **b)** The corresponding selection profile that describes the relative fitness of the average variant ($\int \dot{\tilde{r}} d\tilde{r}$) as a function of the intrinsic Malthusian parameter of that variant ($\tilde{r}$). Populations with $\tilde{r} < \hat{r} - \hat{\epsilon}$ goes extinct because they have negative growth rates on unexploited resources, i.e., $\hat{r} = \tilde{r} + \hat{\epsilon} < 0$.

parameter increases by a rate equal to its additive genetic variance, i.e., that $d\tilde{r}/dt = \sigma^2$. And by eqn 6 the environment deteriorates at the same rate, i.e., $d\epsilon^*/dt = -\sigma^2$. For the population equilibrium $n^* = \hat{r}/\gamma_\alpha = (\tilde{r}+\hat{\epsilon})/\gamma_\alpha$ it follows that $dn^*/dt = d\tilde{r}/dt\gamma_\alpha$ and, thus, that the population equilibrium increases steadily at the rate $dn^*/dt = \sigma^2/\gamma_\alpha$. It can thus be concluded that no equilibrium is expected for the three parameters $\tilde{r}$, ϵ^*, and n. Furthermore, from eqn 5 and the evolutionary increase $d\tilde{r}/dt = \sigma^2$, Fisher's fundamental theorem of natural selection

$$\partial_{ns}r^*/\partial t = \sigma^2 \qquad (10)$$

is obtained, stating that the partial change in r caused by natural selection is equal to the additive genetic variance in r.

The fundamental theorem holds for the case with exploitative competition and a constant genotypic environment because the intrinsic component to fitness is given by the intrinsic Malthusian parameter when competition is purely exploitatively. This is evident from the fitness profile of eqn 7, that is illustrated in Fig. 1a for three populations with different $\tilde{r}$. The fitness profile describes the within population relationship between fitness and a trait. Another profile that is interesting is the relative fitness of the average variant given as a function of the trait value of that variant. This profile is the integral of the selection gradient over the average trait value and, thus, it can be referred to as the *selection profile*. For the case of the fundamental theorem the trait is the intrinsic Malthusian parameter, where the selection profile is obtained by integrating the selection gradient of the average variant (eqn 8) over the intrinsic Malthusian parameter of that variant, i.e., the profile is

$$\int \dot{\tilde{r}} d\tilde{r} \qquad (11)$$

given as a function of $\tilde{r}$. For the case of exploitative competition the selection profile is shown in Fig. 1b. The profile is identical to the fitness profile in the sense that both the fitness of a variant in a population and the relative fitness of the average variant are proportional to the intrinsic Malthusian parameter of those variants.

3 Interference competition

For the case with interference competition the applicability of the fundamental theorem is limited. To see this let the level of interference (ι) represent the number of competitive encounters per individual per unit time, and let it be defined as

$$\iota = \gamma_\iota n \qquad (12)$$

where γ_ι gives the density dependence in ι. Then, to describe the density regulation of the population, eqn 3 can be extended to

$$
\begin{aligned}
r &= \tilde{r} + \hat{\epsilon} - \gamma_\alpha n - \mu \gamma_\iota n \qquad (13)\\
&= \tilde{r} + \hat{\epsilon} - \gamma_\alpha n - \mu \iota \\
&= \hat{r} - \gamma n
\end{aligned}
$$

where μ is the average cost per unit interference, and $\gamma = \gamma_\alpha + \mu \gamma_\iota$ is total density regulation. The constraint of the population equilibrium (eqn 4) applies also to situations with interference competition and, thus, eqns 5 and 6 are also valid. However, the selection pressure on the intrinsic Malthusian parameter is different because

in the absence of interference competition all individuals have access to the same environmental conditions ϵ^*, while with interference competition it are the individuals with the highest competitive ability that have access to the most favourable environmental conditions. Thus, the cost of interference (μ) is inversely related to the competitive ability of the individual implying that the density regulation of the ith variant in the population can be described as

$$r_i = \tilde{r}_i + \hat{\epsilon} - \gamma_\alpha n - \mu \iota - \Delta \mu_i \iota \qquad (14)$$

where the subscript i denotes the ith variant, where terms with no subscript applies to all variants, and where $\Delta \mu_i = \mu_i - \mu$ is the difference in the cost of interference between the ith and the average variant, with μ_i being the cost of the ith variant and μ the cost of the average variant.

As both the competitive ability and the Malthusian parameter of an individual are traits that depend on energy or resource the additive genetic component of the competitive ability is related to the intrinsic Malthusian parameter by a trade-off. Hence, the cost of interference is expected to be an increasing function of $\tilde{r}$ and, thus, for the ith variant in $\tilde{r}$ the deviation in the cost of interference from the average cost can be approximated as $\Delta \mu_i = \mu_i - \mu = \psi(\tilde{r}_i - \tilde{r})$, where ψ is the within population slope between μ_i and $\tilde{r}_i$ at $\{\mu, \tilde{r}\}$, which represents the average variant. Thus, at the population equilibrium the fitness of the ith variant is

$$
\begin{aligned}
r_i^* &= \tilde{r}_i + \hat{\epsilon} - \gamma_\alpha n^* - \mu \iota^* - \psi \iota^* (\tilde{r}_i - \tilde{r}) \quad (15)\\
&= \tilde{r}_i + \epsilon^* - \psi \iota^* (\tilde{r}_i - \tilde{r})
\end{aligned}
$$

with $\epsilon^* = \hat{\epsilon} - \gamma_\alpha n^* - \mu \iota^*$ representing the environmental conditions experienced by the average variant in the population. The selection gradient on the average intrinsic Malthusian parameter is then

$$\dot{\tilde{r}} = \lim_{\tilde{r}_i \to \tilde{r}} dr_i^*/d\tilde{r}_i = 1 - \psi \iota^* \qquad (16)$$

Hence, from the secondary theorem of natural selection (eqn 9) and $dn^*/dt = d\tilde{r}/dt\gamma$, the rates of evolution in respectively the intrinsic Malthusian parameter and the population equilibrium are

$$
\begin{aligned}
d\tilde{r}/dt &= (1 - \psi \iota^*)\sigma^2 \qquad (17)\\
dn^*/dt &= (1 - \psi \iota^*)\sigma^2/\gamma
\end{aligned}
$$

and, by eqn 5, the partial change in the average Malthusian parameter caused by natural selection is

$$\partial_{ns} r^*/\partial t = (1 - \psi \iota^*)\sigma^2 \qquad (18)$$

From eqn 18 it is apparent that the fundamental theorem applies to situations with interference competition only in two special cases. The first case is when the population density is infinitely small, i.e., when $n = 0$. Then the level of interference ι is zero and eqn 18 reduces to the fundamental theorem. The second case is when the competitively superior individuals cannot monopolise the resource. In this case ψ is zero and eqn 18 reduces to the fundamental theorem.

In contrast to the situation with only exploitative competition, the case with interference competition has an evolutionary equilibrium, which is characterised as

$$
\begin{aligned}
\iota^{**} &= 1/\psi & (19) \\
r^{**} &= 0 \\
\hat{r}^{**} &= \gamma/\gamma_\iota\psi \\
\tilde{r}^{**} &= \hat{r}^{**} - \hat{\epsilon} \\
n^{**} &= 1/\gamma_\iota\psi \\
\epsilon^{**} &= \hat{\epsilon} - \hat{r}^{**}
\end{aligned}
$$

where double star indicates the evolutionary equilibrium. Given that the population remains at the population dynamic equilibrium the evolutionary equilibrium of eqn 19 is the global evolutionary attractor. To see this substitute the population equilibrium $n^* = (\tilde{r}+\hat{\epsilon})/\gamma$ into eqn 12 and obtain $\iota^* = (\tilde{r}+\hat{\epsilon})\gamma_\iota/\gamma$. Substitute this expression into eqn 16 and obtain the selection gradient $\dot{\tilde{r}} = 1 - (\tilde{r} + \hat{\epsilon})\psi\gamma_\iota/\gamma$. As the derivative of this gradient $(d\dot{\tilde{r}}/d\tilde{r} = -\psi\gamma_\iota/\gamma)$ is negative for all realistic values of ψ, γ_ι, and γ it follows that the evolutionary equilibrium is the global attractor. When instead the population is off the population dynamic equilibrium, dependent on the parameter values, the evolutionary attractor may be a quasi-periodic cycle (Witting 1997).

The fundamental theorem fails for the case with interference competition because the intrinsic component to fitness is given, not by the intrinsic Malthusian parameter in it-self, but instead by a density and frequency dependent balance between the intrinsic Malthusian parameter and the competitive quality of the replicating unit. It is evident, from the fitness profile of eqn 15 that is illustrated in Fig. 2a, that within population fitness is generally not proportional to the intrinsic Malthusian parameter $\tilde{r}$ for the case with interference competition. For the linear model of this paper, fitness is independent of $\tilde{r}_i$ at the evolutionary equilibrium $\tilde{r}^{**}$, it is positively related to $\tilde{r}_i$ when $\tilde{r} < \tilde{r}^{**}$, and negatively related when $\tilde{r} > \tilde{r}^{**}$. As shown by Fig. 2b, the change in the slope of the fitness profile is reflected in the selection profile by an optimum that corresponds to the evolutionary equilibrium. In contrast to the case
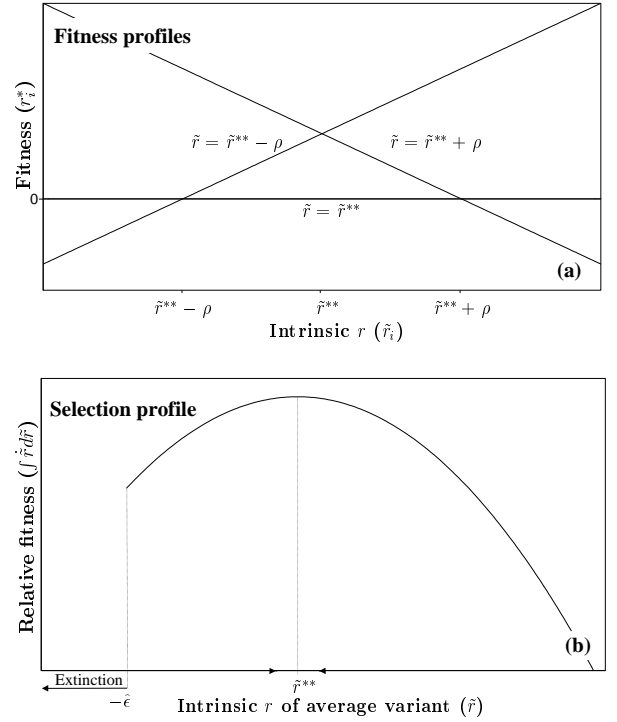

Figure 2: **a)** Fitness profiles, and **b)** the corresponding selection profile for the case with density dependent interference competition. For details see Fig. 1 and the text.

with only exploitative competition, the shape of the fitness profile and the selection profile are different from one another for the case with interference competition.

4   Discussion

The model in this paper is based on the assumption that the regulating terms are linear in r. This is a simplification that affects the quantitative results. However, as populations can be expected to be in population dynamic equilibrium, and as non-linear regulating terms are approximately linear in the proximate surroundings of the population equilibrium, the qualitative results are expected to hold for populations close to population equilibrum. Hence, a partial increase in the Malthusian parameter caused by natural selection can be expected for the case with exploitative competition, while a partial decline may be expected for the case with interference competition. These findings are theoretical results, but what can be expected for natural populations?

In the aim of answering this question consider first the exploitative situation, where the partial increase

in the Malthusian parameter is related to the paradox of a nature in balance. The predicted partial increase imposes an increase in the carrying capacity and a deterioration of the environment. In consequence, for the exploitative case, populations are expected to have high intrinsic growth rates and/or high carrying capacities, while their resources are expected to be over-exploited. The intrinsic growth rates and equilibria of natural populations are though often quite limited, and resources are not necessarily over-exploited. It is well-known that many primary producers are almost unaffected by the presence of herbivores, especially in terrestrial ecosystems where herbivores generally eat less than 10% of the edible plant biomass (e.g., Wiegert and Owen 1971; Ricklefs 1990; Hairston and Hairston 1993).

To explain this paradox of a nature in balance Hairston et al. (1960) proposed and Hairston and Hairston (1993) elaborated the hypothesis that resources are rather unexploited because predators limit herbivores. Dependent upon parameter values this argument may hold for the case with no evolutionary changes. However, on large time scales with selection by exploitative competition the hypothesis of predator limited herbivores requires a Red Queen scenario (Van Valen 1973) where the evolutionary rates in all species are balanced against one another so that there is no overall evolution. The evolutionary rates among species might be balanced in this way in some instances, but there seems to be no reason to expect that a balance be necessarily guaranteed. In the absence of a balance the density of at least one of the involved species is expected to increase in an uncontrolled manner. This is easily seen by applying selection by exploitative competition to Lotka-Volterra predator-prey equations that involve at least three trophic levels (a herb, a herbivore, and a predator). If, in this case, the rate of evolution in the predator exceeds the rate in the prey the predator will eventually over-exploit the prey. If, on the other hand, the rate of evolution is the prey exceeds the rate in the predator, and the herb is easily exploited, the prey is expected to over-exploit the herb.

Due to the general lack of evolutionary balance in trophic systems with only exploitative competition it is understandable that Wynne-Edwards (1962, 1986, 1993) continues to argue that group selection is needed in order to explain the balance of nature. But the conditions for the required type of group selection, where the individuals scarify their own fitness for the benefit of the group, is implausible and for the case with exploitative competition there seems to be no simple solution to the paradox of a natural in balance. This contrasts to the case with density dependent interference competition where the basic prediction of single species models is the evolution of limited population equilibria (eqn 19). Hence, the balance of nature suggests that intra-population interference competition is an important component of the selection pressure on the Malthusian parameter.

A second and independent piece of evidence in favour of the hypothesis of interference competition comes from the joint selection pressure on the Malthusian parameter and the body mass of the organism. As organisms with large body masses generally have evolved from organisms with smaller body masses the correlation between body mass and the intrinsic growth rate and/or the carrying capacity is expected to reflect the selection pressure. If large organisms have evolved by exploitative competition it seems reasonable to expect that they have higher intrinsic growth rates and/or carrying capacities than smaller organisms have. However, the across species allometries document that both the intrinsic growth rates and the population equilibria are smallest in the largest species (Fenchel 1974; Damuth 1981, 1987).

Like the evolutionary equilibrium of eqn 19 can explain a nature in balance, the evolutionary rates of eqn 17 can explain the negative exponents of the allometric relations between body mass and respectively the population equilibrium and the intrinsic growth rate. To see this note that when the level of interference competition is above the level at the evolutionary equilibrium of eqn 19 it follows from eqn 18 that the evolutionary direction is opposite to the direction predicted by the fundamental theorem. Based on the allometric deduction of Witting (1995) it has been shown (Witting 1997) that the evolutionary process of interference competition is expected to stabilise, not at the evolutionary equilibrium of eqn 19, but instead at an evolutionary steady state where the body mass increases exponentially and the level of interference competition is $\iota^* = (4d-1)/(2d-1)\psi$, where d is the number of spatial dimensions in which the organism forages. As this level of interference is larger than the level at evolutionary equilibrium it follows from eqn 18 that the evolutionary direction is opposite to the direction of the fundamental theorem. Thus, by eqn 17, it is predicted that both the intrinsic Malthusian parameter and the population equilibrium decline when the body mass increases. The study of Witting (1997) also showed that the allometric deduction of Witting (1995) apply at the evolutionary steady state and, thus, for organisms that forage in two dimensions, the intrinsic Malthusian parameter is expected to scale to the negative 1/4 power of body mass while the population density is expected to scale to the

negative 3/4 power of body mass. If instead the organism forages in three spatial dimensions the body mass exponents for the intrinsic Malthusian parameter and the population density are expected to be respectively $-1/6$ and $-5/6$ (Witting 1995). These predictions are supported by evidence (Fenchel 1974; Damuth 1981, 1987; Witting 1997, 1998) suggesting that interference competition is an important component of the selection pressure on both body mass and the Malthusian parameter.

If interference competition is an essential factor of the selection pressure on the Malthusian parameter it is only in the two special cases, where either the competitively superior individual cannot monopolise the resource or where the population abundance is infinitely small, that the fundamental theorem applies to natural populations. The limit of an infinitely small abundance is the limit that defines the most basic population dynamic law. In the classical theory of population dynamics the Malthusian law

$$n_t = n_0 e^{\hat{r}t} \tag{20}$$

that predicts an exponential increase in the population density describes this limit (Malthus 1798). This law is based on the assumption of no evolutionary changes in the Malthusian parameter and, thus, it does not apply when there is additive genetic variance in that parameter. In such cases the fundamental theorem defines a new law of hyper-exponential increase. To deduce this law, note that $d\hat{r}/dt = \partial_{ns}\hat{r}/\partial t = \sigma^2$ for constant $\hat{\epsilon}$. Thus, by integrating $d\hat{r}/dt = \sigma^2$ it follows that

$$\hat{r}_t = \hat{r}_0 + \sigma^2 t \tag{21}$$

where $\hat{r}_t$ and $\hat{r}_0$ are the population growth rates at time t and time zero. Thus, $dn/dt = \hat{r}_t n$ is

$$dn/dt = (\hat{r}_0 + \sigma^2 t)n \tag{22}$$

The solution to this equation is the law of hyper-exponential increase in population density:

$$n_t = n_0 e^{\hat{r}_0 t + \sigma^2 t^2/2} \tag{23}$$

Comparing eqns 23 and 20 it is apparent that the rate of increase in population density can be higher than indicated by the Malthusian law, and that the law of hyper-exponential increase reduces to the Malthusian law when the additive genetic variance is zero.

The population dynamic behaviour around the evolutionary equilibrium of interference competition (eqn 19) has been investigated by Witting (1997) for a model with non-overlapping generations. The dynamic behaviour of the model is generally cyclic with periods that coincide with the periods of the cyclic dynamics of forest insects with non-overlapping generations. Cyclic dynamics can be induced by other mechanisms than selection by interference competition, e.g., by predator-prey interactions (e.g., Akçakaya 1992; Hanski et al. 1993; Krebs et al. 1995; Norrdahl 1995; Berryman 1996; Jedrzejewski and Jedrzejewski 1996) or by maternal effects (e.g., Ginzburg and Taneyhill 1994; Inchausti and Ginzburg 1998). But the selection hypothesis seems to be the only hypothesis that from first principles predicts the cyclic sex ratios and body masses that have been observed in populations with cyclic dynamics (e.g., Naumov et al. 1969; Boonstra and Krebs 1979; Stenseth 1982).

If it turns out that interference competition is an essential component of the selection pressure in natural populations it implies that the intrinsic Malthusian parameter and the carrying capacity are inappropriate measures of fitness. This would have severe consequences for our understanding of life history evolution, where the classical theory is based on the assumption that the intrinsic Malthusian parameter and the carrying capacity are appropriate measures of fitness (see Roff 1992; Stearns 1992; Bulmer 1994; Charlesworth 1994). Some of the consequences for the evolution of life history characters are described by Witting (1997) who considers the evolution of body mass, reproductive rate, senescence, ploidy level, sex ratio, sexual reproduction, and eusociality. In the classical theory these characters can be seen as derived traits that are evolutionarily explained by the existence of other, more fundamental, characters. For example, according to the Fisherian sex ratio theory sex ratios evolve from the mating pattern and the ploidy level of the genome (Fisher 1930; Hamilton 1967), and according to the Hamiltonian hypothesis of kin selection eusociality evolves from the presence of kin selection and offspring workers (Hamilton 1964, 1972). With interference competition Witting (1997) concludes that the relationships between derived and fundamental characters tend to be the opposite of the relationships in the classical theory with exploitative competition. With interference competition we can expect that the mating pattern and the ploidy level are evolutionarily determined by the sex ratio, and that kin selection and offspring workers in eusocial species are the evolutionary results of eusociality. Another consequence relates to the evolutionary stability of the evolutionary equilibria. Where the equilibria of exploitative competition tend to be evolutionarily unstable in their fundamental characters, the evolutionary equilib-

ria of interference competition are generally evolutionarily stable (Witting 1997).

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