Major life history transitions by deterministic directional natural selection

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Abstract For large-scale evolution on Earth there has been a directional change where simple self-replicators evolved into large organisms with high metabolic rates and long pre-reproductive periods. Associated with this increase there have been major life history transitions from asomatic, non-senescing, haploid, and asexually reproducing organisms to somatic, senescing, diploid, and sexually reproducing organisms with male and female individuals. Using a game theoretical model it is shown that this trajectory can be explained by deterministic natural selection as it arises from first principles of the self-replication process in mobile organisms. It is shown *i*) that selection for an increase in the energetic state of the organism puts a direction to evolution, *ii*) that selection by density dependent competitive interactions can explain the major life history transitions as a function of the energetic state of the organism, and *iii*) that the two selection processes combined can explain an exponentially increasing body mass. It is also shown *iv*) why, for the case with an increasing body mass, we may expect many life histories to evolve in accordance with the exponents of the body mass allometries, *v*) that an upper constraint on the body mass and metabolic rate can induce an additional transition into eusocial communities, and *vi*) that the evolutionary trajectory is likely reversible with backward evolution during periods of environmental crises.

Keywords: Life history, directional natural selection, competitive interactions, density dependence, major transitions.

1 Introduction

The hypothesis that large-scale evolution is directional has persisted in the biological sciences for centuries. Lamarck (1809) proposed that organisms are driven towards higher levels of perfection. Cope (1871, 1887) and Bonner (1988) that there is an increase in the complexity and size of organisms. Fisher (1930) that the average fitness continues to increase. Vermeij (1987) that organisms become more energy insensitive through evolutionary "arms races". And Maynard Smith and Szathmáry (1995) that hierarchical complexity has increased in a series of major life history transitions where "Entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it". The list of proposed trends is extensive, and reviews are provided by McNamara (1990) and McShea (1991, 1998).

It is widely accepted that some of these trends have played a role in evolution on Earth, but evolutionists of today generally reject that the directions have evolved from a deterministic selection pressure that is inherently part of the natural selection process itself. A deterministic form of natural selection would give a general direction so that independent but similar biotic systems would tend to evolve in parallel. Biotic evolution is instead most often seen as a historical process where evolutionary trends arise as by-products of diffusion processes and random walks (Maynard Smith 1970; Stanley 1973; Fisher 1986). This view seems to be supported by population genetics that describe evolution by the processes of mutation and changes in gene frequencies, with natural selection being a major potential cause for directional changes. But population genetics never provided a set of deterministic selection forces that will explain why evolution on Earth has taken the direction of the major life history transitions, instead of haven taken any other direction.

This lack of determinism has often been seen as something unique that separates natural selection from basically all other fields of the natural sciences. Mayr (1988:20:105), e.g., defines natural selection as "a strictly *a posterior* process ...not controlled by any law". Williams (1992:3) writes that the "term evolution in its original sense of an unfolding or development, analogous to the development of an individual animal, is misleading (Salthe 1989)." "As S. J. Gould (1989:48) forcefully expressed it, if we could rewind the tape of evolutionary history to the remote past and play it again, it would turn out entirely different." And Maynard Smith and Szathmáry (1995:4) conclude that "On the theoretical side, there is no reason why evolution by natural selection should lead to an increase in complexity".

The consensus of historical natural selection supports the Darwinian view that the evolutionary progression should be seen as a tree with all species having a common ancestor. The branching of the tree symbolises the evolutionary diversification of mutation and chance, and this stands in clear opposition to the one-dimensional progress of *scala naturae* that symbolises taxonomy and evolution from Plato to Lamarck. Although the diversification of the evolutionary tree is not in conflict with deterministic directional natural selection (*see below*), it appears that the contrast between *scala naturae* and the Darwinian tree has promoted the view that natural selection is a historical process with no deterministic direction. But taking a somewhat different point of view, the consensus of historical natural selection can instead be seen as the result of an evolutionary theory that has failed to identify the natural selection forces that play the major role in the evolutionary structuring of biotic matter. This view is taken here where I show that major life history transitions in mobile organisms can evolve by a directional trajectory driven by deterministic natural selection, as defined from first principles of the ecological constraints associated with the self-replication process of biotic matter.

The directional trajectory that I deduce relates to large scale evolution, where it can be seen as being superimposed upon the divergence that has occurred among organisms during evolution on Earth. At this level the major life history transitions can be described by a directional trend where simple self-replicators evolved into large organisms with high metabolic rates and long pre-reproductive periods. Associated with this increase there have been transitions from asomatic, non-senescing, haploid, and asexually reproducing organisms to somatic, senescing, diploid, and sexually reproducing organisms with male and female individuals. I aim to show that this evolutionary pattern can be explained as an evolutionary trajectory that arises from the joint action of two natural selection forces. The first is a directional component induced by selection for an increase in the energetic state of the organism, with the energetic state of most organisms being defined by the assimilation of resource. The second force is selection by the density dependent competitive interactions between individuals in populations, a component that can explain the evolutionary transitions as a function of the organism's energetic state (Witting 2002b). In the study I also aim to show how an upper constraint on the body mass and metabolic rate can induce an additional transition into eusocially reproducing colonies and why, for the case with an increasing body mass, we may expect many life histories to evolve in accordance with the exponents of the body mass allometries.

1.1 Levels of directionality

If biotic evolution is driven by deterministic natural selection we may expect that there is nothing particularly unique to the evolutionary trends on Earth. If history was played again we could expect the same overall pattern. It should, however, be noted that directional evolution by deterministic natural selection does not imply a return to a one-dimensional progression like *scala naturae*. It provides instead plenty of possibilities for diversifying evolution on top of the overall direction. This is, among other things, because phenotypic traits evolve in a hierarchical order, where traits at the highest level evolve through the evolution of traits at lower levels. Take, for example, the eye that has evolved on at least 40 different occasions in the animal kingdom (Salvini-Plawen and Mayr 1977). In each case the evolution of the lower-level traits that form the eye have taken a different route, resulting in 40 different designs of the same phenotypic trait; the eye. But, as nearly all mobile animals in light-intensive environments have eyes, it seems that eyes evolve almost deterministically in these organisms, even though the evolutionary design of the eye is better described by a historical process that, among other things, depends on phylogeny and random mutations.

Other factors that allow for evolutionary diversification despite of an overall direction include initial conditions and environmental variation. It is only for cases with completely identical initial, environmental and genetic conditions that we may expect the directions of natural selection to be exactly the same. Dependent upon, e.g., the genetic mutations, the density dependent environment, the extrinsic mortality, the competitive games that evolve, and the spatial dimensionality of the individual's behaviour we can expect differences in the evolutionary trajectories.

Another important factor to note is the difference between short-term and long-term evolution. Even if there is an overall direction to natural selection the evolutionary process will always be historical to the degree that the short-term trajectories will depend on mutations and genetic constraints. But results also suggest that the long-term convergence to a genetic-free equilibrium of Continuously Stable Strategies (CSSs, Eshel and Motro 1981) is independent of the mutation sequence and the genetic structure (Eshel and Feldman 1984; Liberman 1988; Matessi and Di Pasquale 1996; Eshel et al. 1997; Eshel et al. 1998). For the case of a one-dimensional continuity of pure strategies the long-

term convergence to a CSS is deterministic and virtually independent of the distribution of mutations (Eshel et al. 1997). However, for the type of multi-dimensional strategies to be considered in this paper the long-term convergence might depend on genetics (Matessi and Eshel 1992; Matessi and Di Pasquale 1996), although it still remains to be shown whether genetic constraints can prevent a long-term convergence towards the optima of genetic free selection. Given these limitations I use natural selection processes that arise deterministically from the self-replicating process of biotic matter to deduce major life history transitions for long-term evolutionary trajectories at the highest phenotypic level.

1.2 Deterministic natural selection

The origin of natural selection has been defined by the origin of the self-replicating process in the initial self-replicator that arose during the transition from inert to living matter (Michod 1999; but see Lifson and Lifson 1999). Deterministic natural selection may thus be defined as any form of natural selection that arises deterministically from the self-replicating process of the initial self-replicator. In this way it should be possible to deduce any model of deterministic natural selection at any level from the constraints that the physical environment and the initial self-replicator impose on the self-replicating process, including ecological feedbacks like the density dependent constraints that the self-replicating process imposes on the self-replicating process itself. Assuming a stable resource rich environment, I aim for such a model by considering the deterministic directional natural selection that arises from the combined effects of the energetic state of the organism and the density dependence in the competitive interactions between the interacting units in the population, with the interacting units defining the level of selection (Hull 1980).

It is evident that the energetic state of the organism is constraining the self-replication process. This is because the energy of the energetic state can be invested directly in the self-replication process. And for the case where the reproducing units (Witting 2002b), the interacting units and, thus, also the level of selection resemble the asexual self-replicator, it is equally evident that self-replicators in a limited environment induce selection by density dependent competitive interactions. Here the self-replicating process induces population dynamic growth resulting in an increasing density of self-replicators and, thus, also in an increasing number of interactions between self-replicators. And these interactions induce selection for competition and interactive

traits that the self-replicating entities can use to monopolise the resource.

For the more complex cases with interacting and reproducing units at higher levels than the asexual self-replicator, it has been found that higher-level selection processes of density dependent competitive interactions may evolve in mobile organisms from the self-replicating process of the initial self-replicator (Witting 2002b). Here the reproducing units were sub-units of the interacting units, with the interacting units interacting in such a way that the replication rates of the reproducing units are differential. For interacting units with n individual organisms, the reproducing units were groups of $n \geq n/n_\theta \geq 1$ individuals that each contain a single replicating individual and $n/n_\theta - 1$ non-replicating individuals, with n_θ being the number of replicating individuals per interacting unit. The replicating individual is the individual that produces offspring and/or macrogametes, while the non-replicating individuals tend to be males or offspring workers. It was then, dependent upon the energetic state of the organism, found that the density dependent competitive interactions that arises from the self-replication process of the asexual self-replicator can make the individual organisms evolve and organise into reproducing units with respectively pair-wise sexual, co-operative, and eusocial reproduction (Witting 2002b). And for symmetrical parameterisations the competitive interactions, interacting units, and reproducing units were found to evolve to approximately the same level, so that the level of selection tends to evolve to the level of the reproducing unit.

The requirement that deterministic natural selection is deducible from the self-replicating process of the initial self-replicator imposes strong limitations to the type of constraints that can be incorporated into models of deterministic natural selection. In general, the deducibility implies that only the traits of the initial self-replicator, the initial self-replicating process itself, and the constraints that are evolutionarily fixed because they are given by laws that lie outside the domain of evolutionary biology may be incorporated into the life history model (Witting 1997). This contrasts to traditional life history models that are based on historical natural selection (reviewed by e.g., Roff 1992; Stearns 1992; Bulmer 1994; Charlesworth 1994). Here it is the custom to predict the evolution of more derived life history traits from the historical constraints of traits like genetic covariance, phylogeny, and physiological trade-offs that are assumed to be more fundamental. These fundamental traits have often evolved by natural selection themselves, which suggest that they

are evolutionarily modifiable and thus unreliable as predictors for long-term evolutionary processes unless they have themselves been explained from the most basic constraints of the initial self-replicator.

The selection order of the different traits, i.e., the order in which the more derived traits are selected for by the constraints of the more fundamental traits, is given by assumption in traditional models of historical natural selection. This contrasts to models of deterministic natural selection where the selection order can be deduced explicitly from the process of deterministic natural selection. Initially, for the most basic models of deterministic natural selection, each fundamental trait needs to be a trait of the initial self-replicator or a constraint that cannot evolve by natural selection. Then, when some traits have been evolutionarily explained from these most fundamental of all traits, more elaborate models can be constructed where higher order traits can be explained from a larger set of fundamental traits that includes traits that have already been evolutionarily explained by the more basic models. In this way we may construct a hierarchical model system where the selection pressures of the more derived higher-order models are maintained by the lower-order models and the most basic assumption of the initial self-replicating process. And at the limit of perfection the model system of deterministic selection is extended until it explains the evolution of all the traits that have evolved by deterministic natural selection.

The method of deducing more elaborate models and predictions from more basic models is already widely applied in traditional life history theory. But in traditional theory the different fields are usually considered in isolation of one another, generating a set of rather independent sub-theories with each theory dealing with the evolution of specific traits like the sex ratio, body mass, or reproductive rate. The hypothesis of deterministic natural selection requires instead that all sub-fields are part of the same overall theory in the sense that all life history models must be deduced from a common model-web that has ultimately been deduced from the most basic assumptions of the initial self-replicator.

A difficulty tasks with models of deterministic natural selection is to construct the most basic models where the relationships among the different traits reflect only true constraints that cannot be altered by natural selection. A first attempt for such models was developed for mobile organisms by Witting (1997, 2002b), who assumes that life history traits evolve independently of each other unless we have a non-biological law that clearly explains why the different traits should be linked to one another, e.g., through energetic trade-offs. Although this assumption of trait independence may not reflect the true constraints of deterministic natural selection, it might be the best first approach because it prevents that traits be evolutionary explained from constraints that are unexplained and evolutionarily modifiable.

A special problem is models with implicit assumptions that reflect evolutionary modifiable constraints. For deterministic evolution it is essential to aim for models where the implicit constraints resemble the constraining traits before they started to evolve by natural selection. The more derived versions of the constraints may then later be explicitly deduced, or simply added to the model by assumption in order to examine the evolutionary consequences of variation in the constraints. In the latter case the model is no longer a strict deterministic model. But here it is important to keep in mind that all traits may not have evolved by deterministic natural selection. Joint deterministic and historical models may thus be needed in order to explain the evolution of the more complex phenotypes. And in these cases it will generally be the models that contain the fewest unexplained evolutionary constraints that are closest to the purely deterministic models.

1.3 The proposed hypothesis

The directional evolution described in this paper is a sub-model of a larger theory (Witting 1997) that deals with life history evolution by selection by intra-specific density dependent competitive interactions. This theory has shown that the exponents of eight inter-specific body mass allometries may have evolved from the density dependent constraints that competitive interactions and foraging self-inhibition impose on the foraging process in mobile organisms (Witting 1995, 1998). That selection by density dependent competitive interactions can set limits to Fisher's (1930) fundamental theorem of natural selection (Witting 2000a, 2002c), and that it can explain the cyclic population dynamics that have fascinated ecologists for decades (Witting 2000b, 2003), imposing new constraints on the management of natural resources (Witting 2002a). The theory has also shown that multi-level selection by density dependent competitive interactions may generate evolutionary transitions from negligible sized asexual self-replicators to large-bodied organisms with pair-wise sexual, co-operative and eusocial reproduction (Witting 2002b), with the evolution of sex ratios and asymmetrical ploidy levels in eusocial species being deduced from the ecological interactions between the sexual males and females (Witting 1997).

In this paper I aim to integrate these results by an evolutionary increase in the energetic state of the organism. In particular I want to show how the increase in energetic state can generate an evolutionary steady state where the level of interactive competition in the population remains stable while the body mass increases exponentially. And how the increase in energetic state may generate evolutionary transitions from the asexual self-replicator over pair-wise sexual and co-operative to eusocial reproduction. The evolutionary structuring of the organism into these four modes of reproduction is described in detail by Witting (2002b), under the assumption that organisms at the four evolutionary states have populations with different levels of interactive competition. Here I relax this assumption by deducing explicitly the four evolutionary states and their levels of interactive competition by combining the directional increase in energetic state with lower and upper constraints on different life history traits. This was first attempted by Witting (1997), who was criticized for lack of clarity by Kricher (1998). This paper clarifies the original hypothesis by extending it with more traits and by integrating it more firmly into the frameworks of evolutionary stable strategies and multiple levels of selection. Other essential issues that I discuss include a connection between the evolution of exponentially increasing body masses and the evolution of body mass allometries, and the possibility of large-scale reversible evolution where the proposed trajectory runs backward during periods of environmental crisis.

2 The model

2.1 Life histories

Many of the life history traits that separate complex modern organisms from the initial self-replicator at the origin of natural selection can have evolved by the selection pressure of the density dependent competitive interactions within populations. This is exemplified in the present study where a set of traits is selected by competitive interactions to become a set of interactive traits that enhance the organism's interactive quality (or resource holding potential) above the quality of the initial self-replicator. The adult body mass (w), the metabolic rate per unit body mass (B), and the pre-reproductive period (T_p) are the only interactive traits that are modelled explicitly here. The predictions, however, are discussed in relation to a larger set of interactive traits that have been deduced from interactive competition in other studies (Witting 1995, 1997, 2002a,b).

There is selection for the body mass to become an in-

teractive trait when the interactive game allows larger individuals to dominate smaller individuals. And there may also be selection for the metabolic rate per unit body mass to become an interactive trait, because the individuals with the highest metabolic rate can be selected to allocate more energy into competitive interactions than individuals with lower metabolic rates. Behaviour is another interactive trait. If interactive selection on behaviour favours the ability to out-smart other individuals during competition, the individual with the most developed behavioural skills has the potential to out-compete the individual with less developed behaviour. And as time is required to learn and adjust behaviour, there may be selection for the pre-reproductive period to become an interactive trait that is required for the development of interactive behaviour. The mechanisms by which the larger set of traits can be selected to enhance the interactive quality of the organism are discussed by Witting (1997, 2002b).

To define the life history model let the pre-reproductive period T_p, i.e., the period from birth to the age of reproduction, be given by the fraction τ_p of the potential lifespan T, i.e., let $T_p = \tau_p T$. And let $T_r = (1 - \tau_p)T = T - T_p$ be the potential reproductive period that for senescing organisms is the reproductive period of individuals that die of senescence, with $T_r = \infty$ for non-senescing organisms. The pre-reproductive fraction τ_p may then describe how the pre-reproductive period can evolve under the assumption that the pre-reproductive period for otherwise comparable organisms is proportional to the potential lifespan of those organisms. In relation to the learning of inter-active behaviour this assumption is justified by Pearl's (1928) "rate-of-living", where shorter lived organisms live at a faster pace with the rate of organism processes being inversely proportional to the lifespan of the organism.

Let all the energy that an individual uses during the per-reproductive period be supplied by the parents, and let all the energy that an individual uses during the reproductive period be supplied by the individual itself. The latter energetic component is referred to here as the energetic state of the organism, with lifetime energetic state ϵ being the energy (resource) that is used during the reproductive period T_r. Hence,

$$\epsilon^* = \alpha E^* T(1 - \tau_p) \tag{1}$$

where α is the exploitation efficiency, and E^* the resource density at the density regulated population dynamic equilibrium of the exploiting population, with superscript $*$ denoting the equilibrium. Given that the adult body mass after the pre-reproductive period is

constant, the potential lifetime reproductive effort (ϵ_r) is lifetime energetic state (ϵ) subtracted the metabolic use (ϵ_b) of the organism during the reproductive period. Hence, $\epsilon_r = \epsilon - \epsilon_b$, with $\epsilon_b = wBT_r$.

In considering the energetic state ϵ I make a distinction between low-energy and high-energy organisms. High-energy organisms are considered to be organisms for which the energetic state is so high that they, for the proposed selection mechanism, can maintain a body mass in an evolutionary selection equilibrium should the energetic level be stable. Low energy organisms are instead organisms that have so little energy available that they cannot generate sufficient population dynamic growth to induce selection for a body mass in evolutionary equilibrium should the energetic level be stable. At the lower limit of low-energy organisms there is the initial self-replicator that defines the origin of natural selection. For this organism I assume that the interactive traits have the lowest possible values and that the energetic state is so low that the population dynamic growth will just allow the population to persist in a given stable environment.

Let there in accordance with Witting (2002b) be the potential for replicating and non-replicating individuals, with replicating individuals being asexually reproducing self-replicators or sexually reproducing females, and non-replicating individuals being sexually reproducing males or non-reproducing offspring workers. And let me assume that it is only the replicating individuals that contribute energy directly to reproduction so that lifetime reproduction (R^*) of a replicating individual is the lifetime reproductive effort ϵ_r^* divided by the average energy that is allocated into an offspring. The assumption that non-replicating individuals do not directly contribute energy to reproduction is not fulfilled for many species. The assumption is, however, maintained here because it represents the most difficult case to explain, and because the selection mechanism that allows for the evolution of non-replicating individuals not necessarily represents the full set of constraints on the individuals once they have evolved. A direct contribution to reproduction by non-replicating individuals may thus have been selected for by mechanisms that were not involved in the evolution of non-replicating individuals.

Let for the entire pre-reproductive period (T_p) the offspring receive all its energy from the parents, let adult body mass (w) be the mass at the end of T_p, and let body mass and the metabolic rate per unit body mass (B) be defined by energetics. The energy that is allocated to an offspring is then the adult body mass plus the energy metabolised by the offspring during the pre-reproductive period. Given that B is independent of body mass during the growth of the individual, the energy metabolised by the offspring is $qwBT\tau_p$, where $q < 1$ is given by the shape of the body mass growth curve as defined by the relationship between relative body mass w_t/w and relative time t/T_p, with t being time. The parameter q is treated as a constant in this paper, with $q > 0.5$ when the growth curve is convex as expected in nearly all cases (I use the term convex for functions with a negative second derivative).

Pearl (1928) noted that the lifespan of many organisms tends to be inversely related to the metabolic rate per unit body mass of those organisms; just like the longevity of a machine tends to be inversely related to the rate by which the machine is used. This principle of "rate-of-living" has been questioned as representing a too simple model (e.g., Maynard Smith 1958, 1963; Clarke and Maynard Smith 1961a,b; reviewed Rose 1991), nevertheless, the model seems to be sufficiently accurate in relation to body mass allometries where most life history timings, including lifespan, tends to be proportional to the positive 1/4 power of body mass while the metabolic rate per unit body mass (B) tends to be proportional to the negative 1/4 power of body mass (reviewed by Calder 1984). We may thus expect that the body mass components of the allometric relationships for metabolic rate $B = \beta w^x$ and lifespan $T = \tau w^{-x}$ cancel out so that $BT = \beta\tau$, where x is the allometric exponent for metabolic rate. The energy required per offspring can then be approximated as $w(1 + q\beta\tau\tau_p)$, so that the density regulated lifetime reproduction (R) at population dynamic equilibrium $*$ is

$$R^* = \epsilon_r^*/w(1 + q\beta\tau\tau_p) \qquad (2)$$

The model of eqn 2 is applicable to organisms ranging from self-replicators with binary fission to mammalian-like organisms with parental care throughout the entire pre-reproductive period. The model applies to self-replicators if the pre-reproductive period is defined by the interval between binary fission's, the adult body mass is the mass just posterior to the fission, and the growth in mass and increased metabolic expenditure induced by the growth in mass between binary fission's is the energy allocated into an offspring. Hence, it is possible to regard eqn 2 as representing the most basic form of reproduction from which other and more advanced forms may evolve.

Some relationships between eqn 2 and age-structure is given by Witting (1997, 2002b) who describes the density dependent constraint of the population dy-

namic equilibrium $*$ as

$$\lambda^* = pR^* = 1 \qquad (3)$$

where λ is the discrete population dynamic growth rate, p is a survival scalar that is defined from age-structured mortality and assumed here to be density independent. Thus, from the constraints of eqns 2 and 3 we have that $\epsilon_r^* = w(1 + q\beta\tau\tau_p)/p$. And as the energy metabolised by the individual during the reproductive period is $\epsilon_b^* = w\beta\tau(1 - \tau_p)$, from the $\epsilon_r^*/\epsilon_b^*$ ratio we find that

$$\epsilon_b^* = \frac{\epsilon_r^* p\beta\tau[1 - \tau_p]}{1 + q\beta\tau\tau_p} \qquad (4)$$

Then, from $\epsilon^* = \epsilon_r^* + \epsilon_b^*$ and eqns 1 and 4 we find that

$$\epsilon_r^* = \frac{\alpha E^* T[1 - \tau_p][1 + q\beta\tau\tau_p]}{1 + \beta\tau[\tau_p(q - p) + p]} \qquad (5)$$

with $q - p > 0$ when $q > 0.5$ and $R^* \geq 2$. Inserting eqn 5 into eqn 2 lifetime reproduction is

$$R^* = \frac{\alpha E^* T[1 - \tau_p]}{w[1 + \beta\tau[\tau_p(q - p) + p]]} \qquad (6)$$

By eqn 6 the organism can choose to allocate resources either to the interactive traits w, β and τ_p or to the reproductive rate R. For the larger set of interactive traits considered by Witting (2002b) there is a similar trade-off with the reproductive rate. This set contains the interacting unit that is given by n individuals that co-operate in their competitive interactions with other interacting units. Each interacting unit contains $1 \leq n_\theta \leq n$ reproducing units, with each reproducing unit containing a replicating individual and $(n - n_\theta)/n_\theta$ non-replicating individuals. Of the $n_\varphi = n - n_\theta$ non-replicating individuals in the interacting unit, $0 \leq n_\phi \leq n_\varphi$ may be sexually reproducing males while the remaining $n_\omega = n_\varphi - n_\phi$ individuals are sexually or asexually produced offspring workers. The interacting unit may also contain from zero to $n-1$ sexual units, with the sexual unit being defined by a single female replicating individual and from $1/(n-1)$ to $n-1$ sexual males that all mate with the female. Following the model in Witting (2002b), an offspring produced by a sexual unit will receive $n_\phi/(n_\phi + n_\theta)$ proportions of it's genome from the farther/s, and $n_\theta/(n_\phi + n_\theta)$ proportions from the mother. For this larger set of traits it was found that the trade-off between the interactive traits and the average lifetime reproduction of an individual in the interacting unit is

$$R^* = \frac{\alpha E^* T[1 - \tau_p][1 - \phi][1 - \epsilon_\varphi\varphi][1 - (n - 1)z/n]}{w[1 + \beta\tau[\tau_p(q - p) + p]]} \qquad (7)$$

where R is given in replica of the genome in the replicating individual, $\phi = n_\phi/(n_\phi + n_\theta)$ is the proportion of males among the sexual individuals, $0 \leq \epsilon_\varphi \leq 1$ is the fraction of the energy ϵ_r^* that the potentially non-replicating individuals use on competitive interactions and interactive traits instead of replication, $\varphi = n_\varphi/n$ is the proportion of the individuals that are potentially non-replicating, and $0 \leq z \leq 1$ is the tightness of the interacting unit, with $z = 0$ representing the case with no co-operation among individuals and interacting units of single individuals and $z = 1$ the case with completely formed interacting units with n individuals.

In the evolutionary modelling of the traits in eqn 7 I assume that the energetic state evolves independently of the energy allocated into an offspring. This differ from other life history models where it has been assumed that the reproductive rate R is approximately proportional to body mass (e.g., McLaren 1966; Roff 1981, 1986; Gerritsen 1984; Stearns and Koella 1986; Lundberg and Persson 1993). For eqn 2 this would be the case if the energetic state was assumed to scale to the second power of body mass, i.e., if $\epsilon \propto w^2$. But as there seems to be no general non-biological law that will explain this relationship I follow the principle of deterministic natural selection assuming no constraining links between the energetic state and body mass.

The survival scalar p is also assumed to be independent of body mass and this tends to contrast to more traditional models. At the within-population scale in nature the survival rate is often observed to increase with body mass (McGurk 1986), but the assumption has often been that the survival scalar p should decline with body mass because the larger individuals tend to reproduce at a later age (e.g., Bell 1980; Roff 1981; Stearns 1992). However, at larger evolutionary scales, as in between species comparisons, the probability of surviving to the reproductive age may be independent of body mass [Fig. 1 in Witting (1995)]. Also, from an age-structured model we may expect that p is independent of lifespan and absolute reproduction (Witting 2002b) suggesting that p is invariant among organisms with similar bauplans. Thus, in the absence of a clear and general constraint relating body mass to the survival scalar p, I follow the principle of deterministic natural selection assuming independence between p and w.

2.2 Density dependent fitness

Let the density regulation function follow the definition in Witting (2002b), let it operate on the Malthusian parameter $r = \ln\lambda$, and let it for population densities

$N \geq 1$ be given as

$$r = r_m - \gamma \ln N \qquad (8)$$

where $r_m = \ln \lambda_m$ is the maximal population dynamic growth rate. Following Witting (2002b), let the density regulation parameter γ be partitioned into the two components $\gamma = \gamma_\alpha + \mu \gamma_\iota$, where γ_α represents density regulation by exploitative competition, γ_ι density dependence in the level of interactive competition, and μ the cost, or payoff, per competitive interaction. Also let

$$r = r_m - \gamma_\alpha \ln N - \mu \iota \qquad (9)$$

where

$$\iota = \gamma_\iota \ln(N/n) \qquad (10)$$

is the level of interactive competition that reflects the number of competitive encounters per interacting unit per unit time, with n being the number of individuals per interacting unit. As a competitive encounter takes some time, the defined density dependence of ι has a realistic convex shape, while at the same time it ensures logarithmic linearity in relation to the density regulation function of eqn 8. For a more general discussion on density dependent encounter probabilities see Nakajima (2001).

On a discrete time scale the population dynamic growth is

$$N_{t+1} = N_t \lambda_m f(N_t) \qquad (11)$$

where $f(N)$ is the density regulation function that declines monotonically with N. And from eqns 9 and 10 we find that

$$f(N) = n^{\mu \gamma_\iota} N^{-\gamma} \qquad (12)$$

so that the discrete growth rate and the population equilibrium N^* are

$$\lambda = \lambda_m n^{\mu \gamma_\iota} N^{-\gamma} \qquad (13)$$
$$N^* = \sqrt[\gamma]{\lambda_m n^{\mu \gamma_\iota}}$$

Witting (2002a) describes body mass evolution by density dependent competitive interactions for the general density regulation function $f(N)$, while the approximation of eqn 12 is used here for a better comparison with Witting (1995, 1997, 2002b). This approximation will tend not to affect the results in the present paper, because most of the results depend, not on the absolute value of the density regulation function, but on the intra-population slope in the density regulation process around the population dynamic equilibrium. The exception to this is the predicted value for the body mass at evolutionary equilibrium [eqn 29] and evolutionary steady state.

To obtain the fitness profile we can, for the case where competitive interactions and other forms of frequency dependency are absent, insert eqn 2 into $r^* = \ln(pR^*)$ and obtain

$$r^* = \ln \frac{p\alpha E^* T[1 - \tau_p][1 - \phi][1 - \epsilon_\varphi \varphi][1 - (n-1)z/n]}{w[1 + \beta \tau[\tau_p(q-p) + p]]} \qquad (14)$$

where $E^* = EN^{*-\gamma_\alpha}$ and E is the available density of the unexploited resource. Relative to eqn 14 the fitness profile for the case with competitive interactions is biased in favour of the interactively superior interacting units. This fitness bias arises from the payoff of interactive competition (μ) where the interactively inferior units have a higher payoff than the interactively superior units. In general, the payoff of the ith variant is

$$\mu_i = \mu + \Delta \mu_i \qquad (15)$$

where $\Delta \mu_i = \mu_i - \mu$ is the difference in payoff between the ith and the average variant in the population. As a first approximation of the payoff function in the vicinity of the population average for any interactive trait $c \in \{\phi, \epsilon_\varphi, \varphi, n, z, w, \beta, \tau_p\}$ I assume linearity on the logarithmic scale where the payoff of interactive competition is

$$\Delta \mu_i = \psi_c(\ln c - \ln c_i) \qquad (16)$$

where ψ_c is a parameter of the interactive game that describes the within population slope between the payoff of interactive competition and ln interactive quality of trait c. The ψ_c parameter will depend on the evolution of the interactive game, and ψ_c may evolve to be positively related to the level of interactive competition in the population. The symmetrical case where $\psi_c = \psi$ for all c relates to the situation where the competitive game is the same for all interactive traits. Symmetry is quite widespread in evolutionary ecology (Charnov 1993), and similar competitive games may be expected when i) the intra-trait relationship between interactive quality and the value of a trait is similar for all traits, and ii) all traits are equally important in the competitive game.

The assumption of logarithmic linearity implies that the outcome of a competitive encounter be determined by the ratio of the interactive traits of the competing opponents and that the payoff is symmetrical around the population average. For a first approximation, this assumption seems to be more appropriate than linearity with no logarithmic transformation [$\Delta \mu_i = \psi_c(c - c_i)$], where the competitive outcome would be determined by the absolute difference so that a weight difference of, e.g., one gram between two opponents would be

equally important in very large and very small organisms. It does also appear to be more appropriate than a relative term with no logarithmic transformation $[\Delta\mu_i = \psi_c(c/c_i)]$, a case where the payoff function would be asymmetrical around the population average c. And for the interactive traits that are given in proportions, like the proportion of non-replicating individuals (φ), linearity on the logarithmic scale also seem most appropriate because the interactive components of those traits are expressed through absolute quantities like the number of non-replicating individuals in the interacting unit (φn).

Including the effects of interactive competition the fitness profile at population dynamic equilibrium can be given as

$$
\begin{aligned}
r_i^* &= \ln[p\alpha E^* T(1-\tau_p)(1-\phi_i)(1-\epsilon_{\varphi,i}\varphi_i)] \quad (17) \\
&+ \ln[1-(n_i-1)z_i/n_i] \\
&- \ln[w_i(1+\beta_i\tau[\tau_{p,i}(q-p)+p])] \\
&+ \sum_{c\in\mathbf{C}} \psi_c\iota^*(\ln c_i - \ln c)
\end{aligned}
$$

where ι^* is the level of interactive competition at the population dynamic equilibrium, and $E^* = EN^{*-\gamma_\alpha}e^{-\mu\iota^*}$. Note here that the fitness component of interactive competition vanish at the lower limit $\iota^* = 0$ where there is no interactive competition in the population and the fitness profile reduces into eqn 14. Note also that the functional form of the density dependent fitness component of interactive competition has been partitioned into the two terms $e^{-\mu\iota^*}$ and $\psi_c\iota^*(\ln c_i - \ln c)$ in eqn 17, with the first term describing the cost of interactive competition for the average variant and the second term defining the cost of the ith variant relative to the cost of the average variant. This implies that the relative fitness component of interactive competition among the variants in the population is given by the sum on the right-hand side of eqn 17, and that this component vanish in the monomorphic population where $c_i = c$. The relative term vanish in the monomorphic population because it can be expressed only during the direct interactions with the other variants, where the superior variant may monopolise the resource. This contrasts to the relative fitness components of eqn 14 that are absolute components that are expressed also for the case with pure exploitative competition and no interactions among the individuals in the population. In result, the selection pressure of interactive competition is both density and frequency dependent, and the evolutionary equilibration should be deduced by the Evolutionary Stable Strategy (ESS) [Maynard Smith 1982] and the Continuously Stable Strategy

(CSS) [Eshel 1983; Taylor 1989; Christiansen 1991], as described by Witting (2002b) for a fitness profile like eqn 17.

Apart from the frequency dependency of eqn 17, there are other ecological feedback mechanisms that may induce frequency dependent selection. If, for example, there is a constraining relationship between a trait like body mass w and the exploitation efficiency α, variation in body mass is likely to affect resource availability through resource exploitation. And if in the same round, the body mass dependence of the exploitation efficiency show genotype by environment interactions the fitness component of body mass would be frequency dependent. This sort of frequency dependency, however, is not included here where the hypothesis of deterministic natural selection requires a clear-cut constraint that will explain these mechanisms by factors that cannot be modified by natural selection.

2.3 The evolutionary process

The proposed process of directional evolution is driven by selection for an increase in the exploitation efficiency α. This increase provides an increase in the energetic states ϵ that allows for evolutionary transitions between the four evolutionary states that were considered by Witting (2002b). The evolutionary states are i) the downward constrained equilibrium of the low-energy self-replicator and, for high-energy organisms, ii) the evolutionary equilibrium, iii) the evolutionary steady state, and iv) the upward constrained equilibrium.

As described in Section 2.1, the low-energy self-replicator is defined as an organism with an energetic state that is so low that it cannot generate sufficient population dynamic growth to induce selection for a body mass in evolutionary equilibrium should the energetic level be stable. It will be shown that these organisms tend to be situated at a downward constrained equilibrium with interactive traits at their lower limit.

In a high-energy organism with a constant exploitation efficiency the energetic state is instead so high that the population dynamic growth generates interactive competition at levels that select for interactive traits beyond the lower limits of the low-energy self-replicator. For the majority of interactive traits in eqn 17, it turns out that the CSS is given by a function where the equilibrium value of a trait depends on the level of interactive competition in the population [see Witting (2002b) and below]. The body mass, however, is an exception to this rule. As deduced in Section 3.2, the equilibrium conditions for the body mass define both an equilibrium value to the body mass and an equilibrium value

to the level of interactive competition in the population. The overall equilibration is therefore described as a process where the body mass equilibrium determines the level of interactive competition in the population, and where this level subsequently determines the equilibrium values of the other traits through their functional dependence on the level of interactive competition.

For the high-energy organism, the evolutionary equilibrium is a static equilibrium that relates to the case with a stable resource, no additive genetic variance in the exploitation efficiency (α), and life history traits at constant equilibrium values. The evolutionary steady state is instead a dynamic equilibrium that relates to the case where the additive genetic variances in α, w and β are constant and larger than zero, and the energetic level ϵ, the body mass w, and in some cases also the metabolic component β, continue to increase. In this case there will be an exponential increase in α, and compared with the evolutionary equilibrium this increase will cause the reproductive rate to increase because reproduction is a plastic trait that varies with the amount of available resource. And the increased reproduction will cause the population dynamic equilibrium to increase generating increased interactive competition and stronger selection for an increase in the interactive traits. In this process the evolutionary steady state is defined by a balance where the continuous surplus of free energy that is generated by the increasing exploitation efficiency is selected into interactive traits like body mass (w) and metabolic rate (β) leaving the reproductive rate, the population dynamic equilibrium, and the level of interactive competition in a balance of relative stability.

The evolutionary steady state is characterised by a steady state relationship between α, w, and β within the evolutionary lineage in time. At the level of between-species comparisons, such relationships tend to be linear on the double logarithmic scale (Calder 1984; Peters 1983). It is therefore assumed that the steady state relationship can be approximated by the allometric power function

$$\alpha_t = k w_t^a \beta_t^b \tag{18}$$

where k is a constant and the exponents a and b are unknown. In Section 3.2 it will, among other things, be shown that this relationship is compatible with the underlying evolutionary processes, and that the evolutionary steady state is an evolutionary attractor.

At the evolutionary steady state the body mass and metabolic rate will absorb the energy that is added to the organism by the exponential increase in energetic state. This may occur as long as there are no upper

constraints to w and β, and the level of additive genetic variance in those traits is sufficiently large. If instead there are upper limits beyond which the two traits cannot evolve, we have the upward constrained equilibrium where the extra energy is selected into the reproductive rate generating an increased population dynamic equilibrium with an increased level of interactive competition. This equilibrium may be a static equilibrium if the energetic level ceases to increase, or it may be a dynamic equilibrium if the energetic level continues to increase.

3 Results

3.1 Low-energy self-replicator

For the low-energy self-replicator at the origin of natural selection, let the interactive traits take the lowest possible values and let the energetic state ϵ^* be at the lowest level that will allow the population to persist in a given stable environment. At this limit the population dynamic growth rate and equilibrium abundance is so low that we may assume that

$$\iota^{*i} = 0 \tag{19}$$

with superscript $*i$ indicating the state of the initial self-replicator. At this state selection is defined by eqn 14, with a selection gradient that is negative for all interactive traits.

More generally, we may define low energy self-replicators as any self-replicator with an energetic level between that of the initial self-replicator and the lowest level that will maintain a body mass in evolutionary equilibrium. From Witting (2002b) and the results of Section 3.2 it follow that the majority of these organisms will have selection against interacting, reproducing, and sexual units with two or more individuals. Some low-energy self-replicators with energetic levels above the level of the initial self-replicator, however, may have some weak selection for a metabolic component β and/or a pre-reproductive fraction τ_p above the values of the initial self-replicator.

3.2 High-energy organism

Evolutionary equilibrium

To determine the equilibrium for body mass note, from eqns 7 and 3, that the density dependent constraint of the population dynamic equilibrium defines the following relationship $p\alpha E^*T[1-\tau_p][1-\phi][1-\epsilon_\varphi\varphi][1-(n-1)z/n]/w[1+\beta\tau[\tau_p(q-p)+p]] = 1$. We may thus divide

eqn 17 by this expression and obtain

$$
\begin{aligned}
r_i^* = \; & \ln[(1-\tau_{p,i})(1-\phi_i)(1-\epsilon_{\varphi,i}\varphi_i)] \qquad (20)\\
& + \; \ln[(1-[n_i-1]z_i/n_i)w(1+\beta\tau[\tau_p(q-p)+p])]\\
& - \; \ln[(1-\tau_p)(1-\phi)(1-\epsilon_\varphi\varphi)]\\
& - \; \ln[(1-[n-1]z/n)w_i(1+\beta_i\tau[\tau_{p,i}(q-p)+p])]\\
& + \; \sum_{c\in\mathbf{C}}\psi_c\iota^*(\ln c_i - \ln c)
\end{aligned}
$$

with $\mathbf{C}=\{\phi,\epsilon_\varphi,\varphi,n,z,w,\beta,\tau_p\}$. Now, let $c_i{\to}c$ for all $c\neq w$, so that eqn 20 reduces into

$$
r_i^* = \ln(w_i/w)(\psi_w\iota^* - 1) \qquad (21)
$$

with the following selection gradient on ln body mass

$$
\partial r_i^*/\partial\ln w_i|_{w_i=w} = \psi_w\iota^* - 1 \qquad (22)
$$

where $|_{w_i=w}$ indicates that the partial derivative is to be taken at the limit $w_i = w$. Hence, at evolutionary equilibrium $\partial r_i^*/\partial\ln w_i|_{w_i=w} = 0$ the level of interactive competition is

$$
\iota^{**} = 1/\psi_w \qquad (23)
$$

And by inserting eqn 23 into eqn 21 we find that $r_i^{**} = 0$, which implies that all body masses are equally fit at evolutionary equilibrium. Thus, as $r_i^{**} = \ln(pR_i^{**})$ we find that intra-population variation in lifetime reproduction is body mass invariant

$$
R_i^{**} \propto w_i^0 \qquad (24)
$$

if $p_i \propto w_i^0$ as it is suggested in the model section. This result depends on the linear fitness approximation and it may thus hold only in the surroundings of the average body mass.

Consider now the case with density independent interactive competition, a situation that has been studied by Parker (1979, 1983), Maynard Smith and Brown (1986), Abrams and Matsuda (1994), and Härdling (1999). In this case the average body mass declines exponentially when $\iota < \iota^{**} = 1/\psi_w$, it is stable when $\iota = \iota^{**} = 1/\psi_w$, and it increases exponentially when $\iota > \iota^{**} = 1/\psi_w$. The latter increase can only occur up to the limit $w = p\alpha ET[1-\tau_p][1-\phi][1-\epsilon_\varphi\varphi][1-(n-1)z/n]/[1+\beta\tau[\tau_p(q-p)+p]]$, after which the population becomes extinct because $\lambda_m < 1$.

To include density dependence, insert eqn 13 into eqn 10 and find that the level of interactive competition at population dynamic equilibrium

$$
\iota^* = (\gamma_\iota/\gamma)\ln(\lambda_m n^{\mu\gamma_\iota-1}) \qquad (25)
$$

is positively related to the maximal growth rate λ_m. Then, due to the trade-off $\lambda_m = \dot\rho\alpha/w$, where $\dot\rho = pET[1-\tau_p][1-\phi][1-\epsilon_\varphi\varphi][1-(n-1)z/n]/[1+\beta\tau[\tau_p(q-p)+p]]$, from eqn 25 and $\rho = \dot\rho n^{\mu\gamma_\iota-1}$, the level of interactive competition at population dynamic equilibrium is negatively related to the body mass

$$
\iota^* = (\gamma_\iota/\gamma)\ln(\rho\alpha/w) \qquad (26)
$$

The fitness profile of eqn 21 is then

$$
r_i^* = \ln[w_i/w][(\psi_w\gamma_\iota/\gamma)\ln(\rho\alpha/w)-1] \qquad (27)
$$

and the selection gradient with density dependence

$$
\partial r_i^*/\partial\ln w_i|_{\ln w_i=\ln w} = (\psi_w\gamma_\iota/\gamma)\ln(\rho\alpha/w)-1 \quad (28)
$$

This gradient has an evolutionary equilibrium

$$
w^{**} = \frac{\hat\rho\alpha e^{-\gamma/\gamma_\iota\psi_w}}{1+\beta\tau[\tau_p(q-p)+p]} \qquad (29)
$$

where $\hat\rho = n^{\mu\gamma_\iota-1}pET[1-\tau_p][1-\phi][1-\epsilon_\varphi\varphi][1-(n-1)z/n]$. And from eqn 27 and the equilibrium condition $\iota^{**} = 1/\psi_w$, the equilibrium is a neutrally stable attractor because

$$
\begin{aligned}
\partial^2 r_i^*/\partial w_i^2|_{w_i=w=w^{**}} &= (1-\psi_w\iota^{**})/w^{**2} \qquad (30)\\
&= 0\\
\frac{\partial(\partial r_i^*/\partial w_i|_{w_i=w})}{\partial w}\Big|_{w=w^{**}} &= (1-\psi_w\iota^{**}-\psi_w\gamma_\iota/\gamma)/w^{**2}\\
&= -\psi_w\gamma_\iota/\gamma w^{**2}
\end{aligned}
$$

If the population is not at the population dynamic equilibrium the attractor may instead be cyclic population dynamics (Witting 1997, 2000b, 2002a).

From eqn 20 the selection gradient on the metabolic component β is

$$
\partial r_i^*/\partial\beta_i|_{\beta_i=\beta} = (\psi_\beta\iota^{**}-\kappa_\beta)/\beta \qquad (31)
$$

where

$$
\kappa_\beta = \frac{\beta\tau[\tau_p(q-p)+p]}{1+\beta\tau[\tau_p(q-p)+p]} \qquad (32)
$$

For $q-p>0$, which is true when $q>0.5$ and $R^*\geq 2$ [eqn 3], we have that $0\leq\kappa_\beta<1$ and that there is selection for a continuous increase in β, and thus by eqn 29 a decline in body mass, whenever $\psi_\beta\iota^{**}>1\Rightarrow \psi_\beta>\psi_w$, i.e., whenever the metabolic component β is a more important interactive trait than the body mass w. When instead $\psi_\beta<\psi_w$, there is an evolutionary equilibrium

$$
\begin{aligned}
\beta^{**} &= \frac{\psi_\beta\iota^{**}}{1-\psi_\beta\iota^{**}}\frac{1}{\tau[\tau_p(q-p)+p]} \qquad (33)\\
&= \frac{\psi_\beta}{\psi_w-\psi_\beta}\frac{1}{\tau[\tau_p(q-p)+p]}
\end{aligned}
$$

with a positive metabolic rate. And as

$$\partial^2 r_i^* / \partial \beta_i^2 |_{\beta_i = \beta = \beta^{**}} = \tag{34}$$

$$\frac{\partial(\partial r_i^* / \partial \beta_i |_{\beta_i = \beta})}{\partial \beta |_{\beta = \beta^{**}}} = (\kappa_{\tau_p}^2 - \psi_\beta \iota^{**}) / \beta^2$$

the equilibrium is a CSS when $\psi_w > \psi_\beta > \psi_w \kappa_\beta^2$.

From eqn 20 the selection gradient on the pre-reproductive period is

$$\partial r_i^* / \partial \tau_{p_i} |_{\tau_{p_i} = \tau_p} = [\psi_{\tau_p} \iota^{**} - \tau_p / (1 - \tau_p) - \kappa_{\tau_p}] / \tau_p \tag{35}$$

and

$$\partial^2 r_i^* / \partial \tau_{p_i}^2 |_{\tau_{p_i} = \tau_p = \tau_p^{**}} = \frac{\partial(\partial r_i^* / \partial \tau_{p_i} |_{\tau_{p_i} = \tau_p})}{\partial \tau_p |_{\tau_p = \tau_p^{**}}} \tag{36}$$

$$= [\kappa_{\tau_p}^2 - \tau_p^2 / (1 - \tau_p)^2 - \psi_{\tau_p} / \psi_w] / \tau_p^2$$

with

$$\kappa_{\tau_p} = \frac{\beta \tau \tau_p (q - p)}{1 + \beta \tau [\tau_p (q - p) + p]} \tag{37}$$

Hence, there is an evolutionary equilibrium. When $q = p$ the equilibrium is

$$\tau_p^{**} = \psi_{\tau_p} \iota^{**} / (1 + \psi_{\tau_p} \iota^{**}) \tag{38}$$

and it is a CSS that is positively related to ψ_{τ_p} and ι^{**} taking values between zero and one. When $q \neq p$ the evolutionary equilibrium is

$$\tau_p^{**} = \frac{\sqrt{[\psi_{\tau_p} \iota^{**} (y - x) + (y + x)]^2 + 4(\psi_{\tau_p} \iota^{**})^2 xy}}{2 \psi_{\tau_p} \iota^{**} x}$$

$$- \frac{\psi_{\tau_p} \iota^{**} (y - x) - (y + x)}{2 \psi_{\tau_p} \iota^{**} x} \tag{39}$$

where $x = \beta \tau (q - p)$ and $y = 1 + \beta \tau p$. This equilibrium is also positively related to ψ_{τ_p} and ι^{**} taking values between zero and one, and it is a CSS when $\kappa_{\tau_p}^2 < \tau_p^2 / (1 - \tau_p)^2 + \psi_{\tau_p} / \psi_w$ as may be expected in many, if not in most, cases.

Evolutionary steady state

To deduce the evolutionary steady state note that the exploitation efficiency α is not included in the set of interactive traits $c \in \{\phi, \epsilon_\varphi, \varphi, n, z, w, \beta, \tau_p\}$ because it affects fitness only through the exploitative component of eqn 1. To get the selection gradient on α, take the partial derivative of eqn 17 with respect to $\ln \alpha$ and obtain $\partial r^* / \partial \ln \alpha = 1$. Hence, from Robertson (1968), Charlesworth (1990) and Taylor (1996), the exploitation efficiency will increase exponentially as

$$d \ln \alpha / dt = \sigma_{\ln \alpha}^2 \tag{40}$$

where $\sigma_{\ln \alpha}^2$ is the additive genetic variance of $\ln \alpha$. And from eqns 22, 31, and 35 the rates of evolution in body mass, metabolic rate, and pre-reproductive period are

$$d \ln w / dt = \sigma_{\ln w}^2 [\psi_w \iota^{*s} - 1] \tag{41}$$

$$d \ln \beta / dt = \sigma_{\ln \beta}^2 [\psi_\beta \iota^{*s} - \kappa_\beta]$$

$$d \ln \tau_p / dt = \sigma_{\ln \tau_p}^2 [\psi_{\tau_p} \iota^{*s} - \tau_p / (1 - \tau_p) - \kappa_{\tau_p}]$$

where ι^{*s} is the level of interactive competition at evolutionary steady state, and $\sigma_{\ln w}^2$, $\sigma_{\ln \beta}^2$ and $\sigma_{\ln \tau_p}^2$ are the additive genetic variance in the interactive quality of w, β and τ_p at logarithmic scale. Hence, there is an evolutionary increase in w when $\iota^{*s} > 1/\psi_w$ and an increase in β when $\iota^{*s} > \kappa_\beta / \psi_\beta$, while, as determined by eqns 35 to 39 when ι^{**} is exchanged with ι^{*s}, there is an evolutionary equilibrium $0 < \tau_p^{**} < 1$ for the pre-reproductive period. A positive evolutionary equilibrium

$$\beta^{**} = \frac{\psi_\beta \iota^{*s}}{1 - \psi_\beta \iota^{*s}} \frac{1}{\tau [\tau_p (q - p) + p]} \tag{42}$$

is eventually expected for the metabolic component β when $\psi_\beta < \iota^{*s}$ and $q - p > 0$, and this equilibrium is a CSS when $\iota^{*s} > \kappa_\beta^2 / \psi_\beta$.

To see that the evolutionary steady state is an evolutionary attractor note, from eqns 26 and 29, that the level of interactive competition at the population dynamic equilibrium is

$$\iota^* = (\gamma_\iota / \gamma) \ln(\hat\rho \alpha / w [1 + \beta \tau [\tau_p (q - p) + p]]) \tag{43}$$

Thus, if, for a given α_t, $\iota^* > \iota^{*s}$ we have from eqn 41 that w and β will be increasing at a faster rate than expected at the steady state and, then, from eqn 43, that the level of interactive competition will decline toward the level at steady state. If instead, for a given α_t, $\iota^* < \iota^{*s}$ we have from eqn 41 that w and β will be increasing at a slower rate than expected at the steady state and, thus, from eqn 43, that the level of interactive competition will increase toward the level at steady state. The steady state is therefore an evolutionary attractor and the evolutionary process is expected to proceed toward it should the level of additive genetic variance in α, w and β be stable.

To deduce the level of interactive competition at the evolutionary steady state we need to include eqn 18 that describes the relationship between the three traits α, w, and β within the evolutionary lineage in time. At the steady state the evolutionary changes of eqns 40 and 41 need to be compatible with the relationship $\alpha_t = k w_t^a \beta_t^b$ of eqn 18. To determine when this is the case, note from

eqn 18 that $\ln w_t = (\ln \alpha_t - b \ln \beta_t - \ln k)/a$ and thus that

$$\frac{d \ln w_t}{dt} = \left(\frac{d \ln \alpha_t}{dt} - \frac{b \, d \ln \beta_t}{dt} \right) \Big/ a \qquad (44)$$

Then, insert eqns 40 and 41 into eqn 44 to find that the evolutionary process is compatible with the allometric relationship $\alpha_t = k w_t^a \beta_t^b$ when the level of interactive competition at steady state is

$$\iota^{*s} = \frac{\sigma_{\ln \alpha}^2 + a\sigma_{\ln w}^2 + b\sigma_{\ln \beta}^2 \kappa_\beta}{a\sigma_{\ln w}^2 \psi_w + b\sigma_{\ln \beta}^2 \psi_\beta} \qquad (45)$$

Note that ι^{*s} is positively related to κ_β. Thus, due to the positive relationship between κ_β and β [eqn 32], the level of interactive competition at steady state is expected to increase slightly when $d \ln \beta/dt > 0$, and to be stable when $d \ln \beta/dt = 0$.

If the metabolic component β is situated at the evolutionary equilibrium, or if there is no additive genetic variation in the metabolic component ($\sigma_{\ln \beta}^2 = 0$), we have that $d \ln \beta/dt = 0$. Then, from eqn 45, the level of interactive competition at steady state

$$\iota^{*s} = (1 + \sigma_{\ln \alpha}^2/\sigma_{\ln w}^2 a)/\psi_w \qquad (46)$$

is stable for constant additive genetic variances $\sigma_{\ln \alpha}^2$ and $\sigma_{\ln w}^2$, and the body mass will be increasing exponentially at a rate

$$d \ln w/dt = \sigma_{\ln \alpha}^2/a \qquad (47)$$

that is defined by the additive genetic variance in the exploitation efficiency, and not by the additive genetic variance in body mass. This is because the level of interactive competition at steady state is equilibrated by the $\sigma_{\ln \alpha}^2/\sigma_{\ln w}^2$ ratio so that the selection gradient on w is exactly so strong that the body mass can absorb the extra energy that continuously is added to the organism by the evolutionary increase in exploitation efficiency. More generally the extra energy is divided between the body mass and metabolic rate in accordance to the additive genetic variance and interactive importance of those traits.

From eqns 23 and 45 we note that for sufficiently small $\sigma_{\ln \alpha}^2$ and κ_β, and a sufficiently large $\sigma_{\ln \beta}^2$, the level of interactive competition at steady state ι^{*s} can be smaller than $\iota^{**} = 1/\psi_w$ generating a decline in w through an evolutionary increase in β. More generally, however, we expect $\iota^{*s} > \iota^{**} = 1/\psi_w$ and an evolutionary increase in mass. Although κ_β is smaller than one, it is less clear when $\iota^{*s} > \kappa_\beta/\psi_\beta$ and, thus, also whether the metabolic rate will be stable at an evolutionary equilibrium or continuously increasing at an evolutionary steady state.

An important condition for the evolutionary steady state to exist in the proposed form is that the increase in exploitation efficiency α does not result in resource overexploitation through the evolution of a continuously increasing energetic demand of the total population. In order to generate an increase in the energetic state ϵ^*, and thus the potential increase in body mass and metabolic rate, it is essential that the equilibrium density of the resource (E^*) remains relatively stable while the exploitation efficiency increases. And this will only be the case if the relationship between the energetic requirement of the individuals and the equilibrium abundance of the population remains in a balance where the total energetic requirement of the population is relatively stable.

For a life history, population dynamic, and ecological model similar to the one in this paper, a population dynamic balance with a stable E^* has been explained in connection with a deduction of the exponents of body mass allometries (Witting 1995). This deduction was based on the assumption that the level of interactive competition at population dynamic equilibrium (ι^*) is body mass invariant. By eqns 23 and 45 this assumption holds at the evolutionary equilibrium and steady state when the additive genetic variances $\{\sigma_{\ln \alpha}^2, \sigma_{\ln w}^2, \sigma_{\ln \beta}^2\}$, the slopes of interactive payoff $\{\psi_w, \psi_\beta\}$, the exponents $\{a, b\}$, and κ_β are body mass invariant. There seems to be no particular reason to expect body mass dependence in the additive genetic variance at logarithmic scale or in the slopes of interactive payoff. And all the underlying parameters of κ_β [see eqn 32] have been defined as body mass invariant, as it is also the case for the exponents a and b. It thus seems that the allometric exponents deduced by Witting (1995) may apply both across species that are situated at the evolutionary steady state and within a phylogenetic lineage that evolves along the trajectory of the evolutionary steady state. The latter situation resembles the case considered here, suggesting that the resource density E^* is stable at evolutionary steady state.

The level of interactive competition at the steady state with a stable β [eqn 46] is strongly dependent on the exponent a. And from the allometric deduction of Witting (1995) we expect that

$$a = (2d - 1)/2d \qquad (48)$$

where d is the number of spatial dimensions in which the organism forages. Hence, for the symmetrical case $\sigma_{\ln \alpha}^2 = \sigma_{\ln w}^2$, from eqn 48 the level of interactive com-

petition at the evolutionary steady state of eqn 46 is

$$\iota^{*s} = \frac{4d - 1}{(2d - 1)\psi_w} \qquad (49)$$

In this case, from eqn 21, we find that

$$R_i \propto w_i^{2d/(2d-1)} \qquad (50)$$

given $p_i \propto w_i^0$. This implies that the intra-population variation in lifetime reproduction is proportional to the positive 4/3rd or 6/5th power of body mass for organisms that forage in respectively two and three spatial dimensions. More generally, the value of the exponent of the intra-population relationship between reproduction and body mass at evolutionary steady state is not easily deduced, but it can be expected to be positive in most cases.

Upward constrained equilibrium

An upper limit on w and β will be expressed by additive genetic variances $\sigma_{\ln w}^2$ and $\sigma_{\ln \beta}^2$ that approach zero as the trait values approach their upper limits. Hence, from eqn 45, we find that the level of interactive competition at the upward constrained equilibrium be

$$\iota^{*c} \to \infty \qquad (51)$$

with superscript $*c$ denoting the constrained equilibrium. The transition $\iota^{*c} \to \infty$ of eqn 51 indicates the upper theoretical limit to the level of interactive competition. More generally, the transition between the evolutionary steady state $*s$ and the upward constrained equilibrium $*c$ can be seem as a continuum, where the population abundance and level of interactive competition increases with an increase in the ratio of the additive genetic variance in the exploitation efficiency over the additive genetic variance in body mass and metabolic rate. Also, it should be noted that the increase indicated by eqn 51 may not continue indefinitely, especially not if there is an upper limit to the exploitation efficiency α.

4   Discussion

4.1   Deterministic natural selection

I have aimed to explain major life history transitions from deterministic directional natural selection as it arises from first principles of the self-replicating process. Contrary to traditional life history theory, for a given environment extrinsic to the population, this requires a model that incorporates only the constraints

that the physical laws and the traits of the initial self-replicator impose on the self-replicating process. In relation to some life history traits it is relatively straightforward to base the life history model on these constraints, instead of incorporating constraints that have evolved by natural selection. But in other cases I had to compromise in order to get the model to work. One example is in the deduction of the body mass allometries (Witting 1995) where, as empirically documented, I assumed that foraging speed is proportional to lifespan. Other examples are the upper constraints on body mass and metabolic rate that make reproducing units evolve into eusocial colonies. Despite of these limitations the proposed model shows that major life history transitions may likely evolve by the selection pressure that arises from the self-replicating process of the initial self-replicator.

4.2   Major life history trajectory

In conclusion it was shown that deterministic-like natural selection selects for four evolutionary states $\{*i, **, *s, *c\}$ that define four levels of interactive competition $\{\iota^{*i}, \iota^{**}, \iota^{*s}, \iota^{*c}\}$. And for an increase in the energetic state that gives a direction where the initial self-replicator at the origin of natural selection ($*i$) evolves towards the evolutionary steady state ($*s$), with a possible settlement at the evolutionary equilibrium ($**$) or an additional transition into the upward constrained equilibrium ($*c$). The latter two states depend on an upper limit to respectively the energetic level or interactive traits like body mass and metabolic rate.

The transition from the initial self-replicator involves the evolution of a non-negligible body mass, metabolic rate, and pre-reproductive period. These traits are generally in equilibrium at the evolutionary equilibrium. At the evolutionary steady state we can expect an increasing body mass, a stable or increasing metabolic rate, a pre-reproductive period in evolutionary equilibrium, and other life histories that may evolve in accordance with the exponents of the body mass allometries. And at the upward constrained equilibrium, where the body mass and maybe also the metabolic rate are situated at upper limits, we can expect increased interactive competition and an increased pre-reproductive period.

Using a sub-model of the proposed theory, Witting (2002b) showed that the $*i \to ** \to *s \to *c$ transitions select for other life history transitions. The $*i \to **$ transition selects for a transition from a low-energy self-replicator with negligible body mass and asexual reproduction to a high-energy organism with

a non-negligible body mass and pair-wise sexual reproduction between a female and a male. The $** \to *s$ transition selects for a transition from pair-wise sexual reproduction to co-operative reproduction between a sexually reproducing pair and a few sexually produced offspring workers. And the $*s \to *c$ transition selects for a transition from co-operative reproduction to eusocial reproduction between a sexually reproducing pair and up to infinitely many sexually produced offspring workers. In addition, Witting (1997) have shown that the $*i \to \{**, *s, *c\}$ transition may select for a transition from a non-senescing organism with no soma to an organism with soma and senescence. In result it is suggested that the major life history transitions are part of a directional evolutionary trajectory that is expected for mobile organisms in stable resource-rich environments.

There are at least two major life history transitions that have not been included explicitly in my model. The first is the transition from replicators to reproducers (Michod 1983, 1999; Szathmáry and Maynard Smith 1997). Replicators are organisms where the heritable code is given by the structure of the phenotype, which implies that replicators have no distinction between the genotype and the phenotype. Reproducers, on the other hand, are organisms where the heritable unit is only a fraction of the organism so that the genotype and the phenotype are separated from one another. I have not included this dimension in the model because reproducers can be seen as a lower-level phenotypic trait that is necessary for the evolution of large and complex organisms. It seems to be impossible that heritable codes can code for large and complex phenotypes without a separation between the phenotype and the heritable code. The transition from replicators to reproducers may thus be a natural secondary response to selection for large and complex organisms.

The second transition that is not included in the model is from unicellular to multicellular organisms. Like reproducers, multicellularity may be seen as a lower-level trait of large and complex organisms, because it appears to be impossible that large organisms can be functionally efficient without some sort of internal functional differentiation. This differentiation may thus be a natural response to selection for large organisms. And for the hypothesis of selection by density dependent competitive interactions, the multicellular organism is an obvious solution to internal differentiation because the interactive behaviour of the organism can trade-off fitness at the cellular level for fitness at the multicellular level. For more explicit models on multilevel selection for multicellular organisms see Buss

(1987) and Michod (1996, 1997, 1999).

4.3 Major transitions

Although the major transitions considered here are only partial identical with those of Maynard Smith and Szathmáry (1995) the general issues concerning their evolution are the same. Maynard Smith and Szathmáry proposed that an increase in complexity may have been achieved by a series of major evolutionary transitions, where entities capable of independent replication before the transition can only replicate as parts of a larger whole afterwards. They noted that the transitions must be explained in terms of immediate selective advantage, with the problem being that selection acting on entities at the lower level will disrupt integration at the higher level. In the present study it is higher-level selection by interactive competition that favours higher-level integration at the cost of lower-level selection for disintegrated entities, with the strength and level of higher-level selection increasing with increasing levels of interactive competition. Thus, for the transitions $\iota^{*i} \to \iota^{**} \to \iota^{*s} \to \iota^{*c}$ higher-level selection is able to outbalance increasing levels of lower-level disruptive selection, favouring higher levels of integration in populations with higher levels of interactive competition [see Witting (2002b) for details on the trade-offs].

The hypothesis of deterministic natural selection implies that not only must the evolution of the transitions be explained by immediate selection, but the long-term maintenance will also have to be explained by immediate selection because otherwise the system should evolve to another state. This is in some contrast to the transitions envisioned by Maynard Smith and Szathmáry (1995), who suggest that higher-level entities are maintained by contingent irreversibility and/or by central control. They suggest, e.g., that the absence of parthenogenesis in mammals is due to some genetic constraint. The hypothesis of deterministic natural selection suggests instead that parthenogenesis is more absent in mammals than in most other mobile sexual organisms because mammals are exposed to a more persistent selection pressure for sexual reproduction. Under the hypothesis of density dependent competitive interactions this would, e.g., be the case if the abundances of mammals were more stable at the population dynamic equilibrium than the abundances of other animals. This might be the case if endotherm animals are better to buffer against environmental variation than exotherm animals.

4.4 Directional drive

While Szathmáry and Maynard Smith (1995) concluded that organisms on Earth have become more complex over time, they had "no theoretical reason to expect evolutionary lineages to increase in complexity with time". The present study shows instead that we do have theoretical reasons to expect that some of the major evolutionary transitions are part of a directional trajectory caused by deterministic natural selection and, thus, that these transitions may be expected to be general principles of unconstrained long-term evolution.

The proposed directional drive is given by the general principle that, other things being equal, there should be selection for an increase in the energetic state of the organism. This principle was probably first noted by Vermeij (1987, 1994) who proposed that organisms become more energy intensive, or escalated, over time. He also noted the widespread importance of interactive competition, but none of his hypotheses were formulated into explicit mathematical models.

Since the theoretical work of Parker (1979, 1983) it has been known that interactive competition may result in "arms races", where directional evolution arises from selection for interactive traits that enhance the "resource holding potential" of the organism (Simpson 1953; Dawkins and Krebs 1979; Parker 1979, 1983; Haigh and Rose 1980; Maynard Smith 1982; Maynard Smith and Brown 1986; Brown and Maurer 1986; Vermeij 1987; Härdling 1999). But the directional evolution predicted by arms races apply only to the restricted case where the level of interactive competitive is sufficiently large and density independent (Abrams and Matsuda 1994) and the cost increases linearly or slower than linearly with the trait (Härdling 1999). Here the population is expected to evolve toward extinction because the increase in the interactive traits absorbs energy from the reproductive rate causing the population equilibrium to decline towards zero (Parker 1983).

In the more realistic case where the competitive interactions are density dependent, there is no long-term direction to evolution by interactive competition when the energetic state is stable. This is because the interactive traits will stabilise at intermediate levels as competition is relaxed when the population equilibrium decreases (Abrams and Matsuda 1994). But with the continuous increase in energetic state predicted in this paper, interactive traits like body mass and metabolic rate can continue to increase. This is because the energetic increase can maintain the level of reproduction and interactive competition at constant levels, while at the same time there is free energy to be selected into the mass and/or metabolic rate.

4.5 Increase in body mass

The predicted increase in body mass at evolutionary steady state provides an explanation for Cope's rule (Cope 1871) of body mass increase in phylogenetic lineages. This rule has often been misunderstood (McKinney 1990), and it is important to note that it should not necessarily be seen as a principle of size increase in all evolutionary lineages. Jablonski (1997), e.g., has shown that it fails as a general principle within the lineages of Cretaceous molluscs. But instead of being a principle of size increase in all lineages, Cope's rule may be seen as a principle of increase in the maximal size of a taxon (Stanley 1973; McKinney 1990), a pattern that Gould (1988) has described as an increase in variance.

An increase in the maximal size together with the absence of a clear trend for body mass increase in the majority of evolutionary lineages, does not necessarily imply the absence of an overall selective advantage to body mass (McShea 1994). The absence of a clear trend may instead result from the joint action of a many scale dependent factors. But nor does an increase in maximal size necessarily imply the action of underlying directional selection. The increase may instead be a reflection of random evolutionary diffusion away from some lower limit on size (Stanley 1973). The energetic trade-off of eqn 2 between body mass and reproduction, however, implies that one of the most basic expectations of deterministic natural selection is strong selection for a decline in body mass. In this perspective we expect that the large body masses on Earth must be maintained by some selective advantage to body mass, rather than being a reflection of neutral non-selective evolution.

For the proposed theory there are plenty of reasons to expect that the predicted increase in body mass may not apply to all organisms. The prediction of an exponentially increasing body mass is based on unconstrained evolution in a stable resource-rich environment. But in many, if not in most, cases we may expect environmentally imposed limits to the amount of resource that the organisms can consume. And as these limits will be specific for each species we can expect natural organisms with a variety of energetic levels and body masses. And if the available resource is extremely sparse the upper limit to resource consumption may be so low that the organism cannot even evolve away from the low-energy self-replicator. Such low-energy self-replicators may also be unable to invade environments with more abundant resources if these are dominated

by high-energy organisms that exclude the low-energy organisms by direct inter-specific interactive competition. In this way diverse patterns may arise even in cases where there is an underlying direction to natural selection.

The proposed model indicates that it may be possible to use the intra-population relationship between reproduction and body mass to estimate whether a population is situated at an evolutionary equilibrium with a stable body mass or at an evolutionary steady state with an exponentially increasing mass. In the classical life history theory that disregards the effects of interactive competition it is the custom to use a proportional increase in reproduction with body mass as a force that selects for an increase in body mass (McLaren 1966; Case 1979; Roff 1981; Gerritsen 1984; Stearns and Koella 1986; Lundberg and Persson 1993). The proportional relationship is left unexplained in the classical theory, but for some parameterisations the model presented here predicts the relationship from the evolutionary equilibration in body mass. When the body mass is in evolutionary equilibrium and $p_i \propto w_i^0$, lifetime reproduction is expected to be independent of body mass [eqns 24 and 50]. But when the organism is situated at the evolutionary steady state with a stable β, lifetime reproduction is expected to scale as $R_i \propto w_i^{\iota^{*s}-1}$, with $\iota^{*s} - 1$ reducing to $\approx 4/3$ in organisms that forage in two spatial dimensional and $\approx 6/5$ in three-dimensional foragers given that $\sigma_{\ln\alpha}^2 \approx \sigma_{\ln w}^2$ and $p_i \propto w_i^0$.

From empirical studies it is known that the exponent k is positive in most species (Reiss 1989; Peters 1983). Wooton (1979) estimated an average k of 1.2 for 62 species of fishes, as predicted by the evolutionary steady state $\sigma_{\ln\alpha}^2 \approx \sigma_{\ln w}^2 \gg \sigma_{\ln\beta}^2$ if we assume that fishes forage in three spatial dimensions. Peterson (1950) estimated a k of 1.03 in spiders, Robertson (1957) that $k \approx 1$ in *Drosophila melanogaster*, and Ridely and Thompson (1979) a k of 0.77 for five species of Asellus (Crustacea; Isopoda). This suggests that many populations may be closer to the evolutionary steady state than they are to the evolutionary equilibrium and, thus, that their average body masses may increase exponentially. More direct evidence can be found for some lineages in the fossil record. The record of fossil horses (MacFadden 1986), e.g., shows that the body mass can increase exponentially over millions of years (Witting 1997).

4.6 Backward evolution

In other cases we can expect a decline in body mass. For the proposed model a species may dwarf if its indi-

viduals have progressively less resource available. Then, the rate of reproduction will decline causing a decline in the population dynamic equilibrium and the level of interactive competition. And the latter decline can select energy from body mass to numerical replication generating a decline in body mass. This means that a species may dwarf in a stable environment if a larger species invades and excludes the first species from the main habitat so that it will have to live in habitats of lower quality. In the same way, we can expect widespread dwarfing if the primary production or the availability of resources continues to decline over a longer period of time.

But it may not only the energetic state and body mass that will be affected by a decline in the available resource. This is because all the interactive traits of the major life history transitions can have evolved by selection by interactive competition. A decline in interactive competition caused by a continuously declining resource may then affect all traits resulting in backward evolution toward the simple self-replicator at the origin of natural selection. In this way it is suggested that the major life history trajectory is reversible with the actual direction being defined by environmental conditions.

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