

The major evolutionary transitions as a deterministically unfolding process

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Abstract

During evolution on Earth there has been a directional change where simple self-replicators have evolved into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. Associated with this increase there has been a transition from an asomatic, non-senescing, haploid, and asexually reproducing organism to a somatic, senescing, diploid, and sexually reproducing organism. In a few special cases there have been an additional transition to two different forms of eusociality. A new theory of natural selection (Witting, 1997a) suggests that this directional increase in complexity is the evolutionary process to be expected in a stable environment. An essential component of the theory is selection by density dependent competitive interactions, a factor that is not included in classical life-history theories. It is discussed how it is possible to integrate the classical and the proposed theory to obtain a more general theory of evolution.

Introduction

Witting (1997a) describes how the selection pressure of density dependent competitive interactions can be used to build a single mathematical model that can deduce the evolution of the major life histories in mobile organisms. The theory proposed is, to the best of my knowledge, the first theory that suggests that evolution by natural selection is inherently directional in the sense that simple self-replicators in a stable and favourable environment automatically evolve toward the complex organisms on Earth.

The proposed theory is related to the major evolutionary transitions in the way that the simple self-replicator goes through the major evolutionary transitions when it evolves toward more complex organisms predicted by the theory. Moreover, in the proposed theory the transitions are part of a deterministic process that is driven by natural selection. This result that is quite different from the initial proposal of Maynard Smith & Szathmary (1995) where the increase in complexity is given, not by natural selection, but instead by a historical process. The purpose with this talk is to give a brief overview of some of the essential components of my theory, and to compare the theory to the classical life-history theory, which is reviewed in the books of Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994). But first I will briefly describe the evolutionary transitions that are explained by the theory.

The major evolutionary trajectory

I prefer to describe the major transitions as a directional change, i.e., as a major evolutionary trajectory that summarises the evolutionary process at a very large scale. From empirical evidence we know that evolution on Earth have included a directional change where simple self-replicators have evolved into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. And the increase in body mass has been associated with life-history traits that evolve in concordance with the exponents of the body mass allometries. A comparison between prokaryotes and the higher eukaryotes suggests furthermore that the transition from a negligible to a relatively large body mass is associated with an evolutionary transition from a haploid organism with no soma, no senescence, and no sexual reproduction, to a diploid organism with soma, senescence, and sexual reproduction between a male and a female. In a few special cases, mostly in insects, there has been an additional transition into eusocial communities, a transition that in some instances seems to coincide also with a transition from a diploid to a haplodiploid genome. It is this evolutionary scenario that the proposed theory deduces from first principles of the self-replication process.

The proposed theory

The proposed theory describes evolution by natural selection as an optimisation process that is not constrained by phenotypic constraints. This is unlike classical life-history theory where all the evolutionary predictions that I am aware of depend on the presence of such constraints. A well-known example is the classical theory of senescence where the evolution of senescence depends on the presence of a soma. In contrast to this I have aimed at a theory where the only allowable constraints are *i*) the process of self-replication (i.e., the definition of life), and *ii*) the physical and ecological constraints that cannot evolve by natural selection. The essential idea is then to deduce the major evolutionary trajectory from these first principles.

From these first principles we expect two different forms of selection. The first force arises from the exploitation of the resource where, other things being equal, it is the individual with the highest exploitation efficiency that can have the highest fitness because it has more resource available for reproduction, survival, and/or competitive quality. The second force is the selection pressure that arises from the density dependent competitive interactions that are unavoidable among the individuals in natural populations.

These two modes of selection are all we need to explain the major evolutionary trajectory, and together they define the limited or special version of the proposed theory. There is also a general version of the theory that includes a third force of selection that arises from an intrinsic optimisation of the phenotype. This latter version of the theory can be seen as an integration between the classical life-history theory and the special version of the proposed theory. I will first describe how the special version is formed from the selection pressure of exploitation and competitive interactions, and then describe how the general version is formed by the integration between the two theories.

The first two forces of selection play two distinctively different roles: Selection by exploitation induces a direction to the evolutionary process, where the organism experiences an increase in energetic quality, i.e., an increase in the amount of resource or energy that it can assimilate from the environment. Selection by density dependent competitive interactions, on the other hand, can explain the allocation of the assimilated resource among the different life-history traits. And when the two forces are combined we obtain the phenotypic transitions known from the major evolutionary trajectory.

Life-histories determined by competitive interactions

Let me first explain how density dependent competitive interactions can explain the life-histories contained in the major evolutionary trajectory. Among other things, these life-histories include the reproductive rate, the metabolic rate, the mental capacity, the body mass, and the body mass allometries describing the power relations between body mass and other traits like the rate of reproduction, the metabolic rate, the lifespan, the intrinsic growth rate, the population density, and the home range area. Apart from these continuous traits the trajectory includes also a set of more or less discrete traits containing soma, senescence, males, sexual reproduction, the ploidy level of the genome, and eusociality.

A common feature of most of these traits is that they can represent competitive quality in the sense that the traits can be used to dominate conspecifics during competitive encounters, or at least that the traits can be associated in one way or the other with this form of competitive quality. For example, other things being equal, we expect that a large individual can dominate a small individual, that an individual with a high metabolic rate can dominate an individual with a low metabolic rate, that the clever can cheat the stupid, that a male can dominate a female (if we define a male as an individual that allocates resource to competitive quality at the cost of reproduction), that a pair can dominate a single individual, and that an eusocial colony can dominate a pair. Moreover, we expect that both senescence and soma correlate positively with competitive quality in the sense that an individual that allocates resource to competitive quality at the cost of self-repair can dominate an individual that does the opposite. And finally we expect that the degree of sexual reproduction, described either by the ploidy level of the genome or by the fraction of the offspring's genome that comes from the father, correlates positively with competitive quality. This is because in the presence of competitive interactions we expect that the female will choose the males that are competitively superior, and that the competitively superior males will dominate the inferior males in order to have access to the females that allocate the largest fraction of the males genome on to their offspring. In this way it are the females that allocate the largest fraction of the male's genes to the offspring that are expected to have the highest competitive quality.

Apart from these traits of competitive quality the life-history is described also by the intrinsic growth rate that is given by the demographic rates (reproduction and survival). For an organism at a given energetic level, there is a trade-off between competitive quality and the demographic rates so that the two components are inversely related to one another. Hence, the life-history can be described as a balance between the demographic rates and the competitive quality, and the evolutionary determinants of this balance depends on the level of intra-population interference, i.e., on the number of competitive encounters per individual per unit time. If this level is high, the life-history will be biased in favour of competitive quality at the cost of the demographic rates, while the life-history will be biased in the other direction when the level of interference is low or absent.

Evolutionary transitions determined by energetic quality and constraints on body mass

Based on these principles it follows that the major life-histories are given by the level of intra-population interference, and it turns out that this level is functionally determined by the energetic quality of the organism and by the evolutionary determinants of the body mass.

This function behaves in a step wise manner, containing three well defined steps: *i*) At the lower step the energetic quality of the organism is extremely low, there is close to zero interference, and a negligible body mass. *ii*) At the intermediate step the energetic quality of the organism is relatively large, there is a relatively high and well-defined level of interference, and a relatively large body mass. *iii*) The upper step resembles the intermediate step, but the

body mass is sitting at an upper evolutionary constraint while the level of interference is much larger, maybe even infinitely large.

The interesting results are then, that when all this is described mathematically and the optimal life-histories are deduced from the first principles of the two first steps of this function, then we obtain the evolutionary transition that exists between prokaryotes and viruses on one side and the higher mobile eukaryotes on the other side. That is, we predict that low energy organisms have a negligible body mass, that they do not senesce, that they have no soma, that they are haploid, that they contain no male individuals, and that they reproduce asexually. On the other hand we predict that high energy organisms in stable environments have a relatively large body mass that continues to increase, that they experience senescence, that they have a soma, that they are diploid, that they contain male individuals, and that they reproduce by the usual form of sexual reproduction where half of the genes in the offspring come from the mother while the other half come from the father. The evolutionary increase in body mass in this latter group reflects the directionality of the evolutionary process, where the extra energy that is available from the evolutionary increase in the exploitation efficiency is continuously selected into the body mass. Moreover, for the high-energy organisms we obtain the exponents of the body mass allometries from first principle of a foraging process that is optimised by natural selection.

When instead the optimal life-history is deduced from the last two steps of the interference function, then we obtain an additional transition from pair wise reproduction into eusocial breeding. And finally within the eusocial group the transition between termites on one hand and ants/bees on the other is given as a function of the functional role played by the sexual male. That is, if the function of the male is restricted to sexual behaviour then the eusocial colony is like an ant/bee colony with a female biased sex ratio, a worker caste containing only female offspring, and a haplodiploid genome. If instead the sexual male form a pair with the sexual female we obtain a termite like colony with an even sex ratio, a worker caste containing both female and male offspring, and a diploid genome.

Comparing with classical life-history theory

To the best of my knowledge the proposed theory is the first theory to explain most of the major life-histories in mobile organisms from the selection pressure of density dependent competitive interactions. However, the theory is not the only theory dealing with the evolution of these characters. Especially the classical life-history theory, that we all are so familiar with from the review books of Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994), have been developed into a mature theory covering the evolution of nearly all life-histories.

Although these two theories deal with the evolution of the same characters they differ considerably in the proposed mechanisms. Where the essential force explaining the life-histories in my theory arises from the action of density dependent competitive interactions, the classical theories generally disregard competitive interactions dealing instead with natural selection as an intrinsic optimisation that is defined from the phenotypic constraints intrinsic to the organism.

So we are now in the peculiar situation that we have two distinctively different theories deal with the evolution of the same life-history traits. The evident question is then on what scales the two theories apply. It seems that the classical theory cannot stand alone at an evolutionary scale where we are interested in the evolutionary stability of the predicted equilibria. This is because the classical equilibria are evolutionarily stable only when the phenotypic assumptions that underlie the classical predictions are selectively neutral or optimal under the type of selection that is defined by the classical framework. However, as described in more detail by Witting (1997a,b), under the action of the classical form of selection the classical assumptions

are evolutionarily unstable implying that the classical predictions collapse to that of small and simple self-replicators. An example is Lack's clutch size that is evolutionarily unstable because the classical form of selection selects against the trade-off between reproduction and survival. The result is a continuous increase in reproductive rate. An other example is the Fisherian sex ratio theory that is evolutionarily unstable because the two fold cost of the male selects against the male individual generating an evolutionary optimum that has no males and, thus, also no sex ratios.

However, if we superimpose the intrinsic selection procedures of the classical theory on top of the proposed theory it is generally possible to obtain the classical equilibria in an improved form where they are evolutionarily stable. These equilibria differ from the original equilibria in the sense that they explain not only the evolution of the original predictions but also the evolution of the phenotypic assumptions that underlie the classical predictions. Another difference is an almost complete change in the evolutionary causality that generates the evolutionary stability of the predicted equilibria. For example, in the traditional version of Lack's clutch size it is the optimal rate of reproduction that evolves from a trade-off between reproduction and survival, while in the new version it is instead the trade-off that evolves from the optimal rate of reproduction. In the same way, in the classical or Fisherian sex ratio theory it is the sex ratio that evolves from the ploidy level of the genome, while in the new theory it is the ploidy level that evolves from the sex ratio.

Although there is a conflict between the ways we interpret evolutionary causality in the two life-history theories, there is, on a closer examination, no real conflict at the mathematical level where the two theories can be integrated into a single unifying theory. In fact, in instantaneous points and in the surroundings of the evolutionary equilibria the mathematical framework of the proposed theory tends to converge into the mathematics of the classical theory. In this way the classical theory can be seen as a local approximation that holds as long as we examine only the selection pressure within species.

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