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## Time and Fitness in Evolutionary Transitions in Individuality

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| <b>Abstract:</b>                                     | <p>It is striking that the concept of fitness although fundamental in evolutionary theory, still remains ambiguous. I argue here that time, although usually neglected, is an important parameter in regards to the concept of fitness. I will show some of the benefits of taking it seriously using the example of recent debates over evolutionary transitions in individuality. I start from Okasha's assertion that once an evolutionary transition in individuality is completed an ontologically new level of selection emerges from lower levels of organization. I argue that Okasha's claim to have identified two ontologically distinct levels of selection is an artifact created by an undeserved comparison between the fitness of the collective level and the fitness of its constituents. Once fitness is assessed over the same period of time at the two levels of organization it becomes clear that only one, unique process of selection is acting upon both levels.</p> |

# Time and Fitness in Evolutionary Transitions in Individuality

## *Abstract*

*It is striking that the concept of fitness although fundamental in evolutionary theory, still remains ambiguous. I argue here that time, although usually neglected, is an important parameter in regards to the concept of fitness. I will show some of the benefits of taking it seriously using the example of recent debates over evolutionary transitions in individuality. I start from Okasha's assertion that once an evolutionary transition in individuality is completed an ontologically new level of selection emerges from lower levels of organization. I argue that Okasha's claim to have identified two ontologically distinct levels of selection is an artifact created by an undeserved comparison between the fitness of the collective level and the fitness of its constituents. Once fitness is assessed over the same period of time at the two levels of organization it becomes clear that only one, unique process of selection is acting upon both levels.*

## **1. Introduction**

*Yes, fitness is the central concept of evolutionary biology, but it is an elusive concept. Almost everyone who looks at it seriously comes out in a different place.*

*Leigh Van Valen 1989,2-3*

It is striking that the concept of fitness, although fundamental in Darwinian Theory, is not yet unified, and after more than 150 years still remains ambiguous. Is fitness an ecological descriptor or a mathematical predictor? Do species have a fitness, and if they do, how shall we measure it? Should fitness be measured over short or long periods of time? All these questions are still without clear answers. In this article, I have two aims. First, I will clarify the concept of fitness by arguing that time is an important parameter of this concept. Discussions over the concept of fitness are numerous and I will not be able to cover them all. Rather, I will concentrate on particular benefits that pairing the concept of fitness with time can bring to one contemporary discussion over the levels of selection, namely evolutionary transition in individuality (ETI). I will demonstrate, and this will be my second aim, that the model of ETIs developed by Okasha (2006), relying on Michod and colleagues' work, faces a serious problem. This problem, I will argue, comes precisely from the fact that in his model Okasha does not sufficiently take time into account when measuring fitness at different levels of organization.

ETIs are events in the course of evolution that lead to the formation of new higher level individuals due to the cooperation of two or more individuals at a lower level of organization (Michod 2011). One example of ETI is the transition from uni- to multicellular organisms. A number of other ETIs have been proposed, among them the transitions from prokaryote to eukaryote cells, from unicellular to multicellular organisms, and from multicellular organisms to integrated colonies such as colonies of ants or honeybees. One of the most accomplished models of ETI is the one suggested by Michod and colleagues. In a number of articles and books (Michod 1999, 2005; Michod, Nedelcu, & Roze 2003; Michod, Viossat, Solari, Hurand, & Nedelcu 2006) they propose a number of conditions for ETIs to occur. Okasha (2006, 2011) recently set Michod and colleagues' work in the framework of Multilevel Level Selection 1

(MLS1)/ Multi Level Selection 2 (MLS2), which was initially developed by Damuth and Heisler (1988).

Okasha's and Michod's models of ETIs are committed to a concept of fitness which is measured by the ability of a given entity to survive and reproduce in its environment. According to this definition, the higher the survival and reproductive rate of this entity, the higher its fitness is. Although such definition is somewhat restrictive and does not cover the whole range of possibilities which can be embraced by the concept of fitness, I will accept it as common ground for the development of my arguments, which will run as follows. In Section 2, I will briefly review Michod and colleagues' as well as Okasha's models of ETIs in regards to fitness. I will present two specific claims defended by both authors: (1) that during the last stage of an ETI, once a division of labor is in place, the fitness of the components constituting the newly emerged individual reaches zero; (2) that there are two fundamentally distinct processes of selection, namely multilevel selection 1 (MSL1) and multilevel selection 2 (MLS2), occurring alternately at the different stages of an ETI. Claims (1) and (2) are slightly different versions of what is called the export-of-fitness view on ETI. Claim (1) has been recently criticized by Godfrey-Smith (2011, 77-78) for its metaphorical nature. Although this criticism deserves a more thorough examination, that will not be done in this article. In Section 3, I turn to claim (2) and demonstrate that if fitness is assessed over the same period of time at the collective level and at the level of its constituents, then there is commensurability between these two models of selection. For that reason, they cannot represent two ontologically distinct processes of selection, but are ways to describe the same process from the perspective of two spatial and two temporal scales. However, I do not deny the epistemological value of describing ETIs within the MLS1/MLS2 framework and will examine the reasons for this.

## **2. Michod and Okasha on evolutionary transitions in individuality**

Michod and colleagues propose the following model of ETI. For new individuals at a higher level (“collective” level) to emerge from a lower level (“particle level”)<sup>1</sup>, e.g. for multicellular organisms to emerge from unicellular organisms, two things must happen. First, conflicts between members of the collective need to be eliminated. Conflicts can be resolved in different ways such as for instance policing mechanisms and developmental bottlenecks, to name two of them. They both promote genetic homogeneity and consequently reduce competition between the different members of a group. However, even if genetic homogeneity is reached between the different members of the same group, this will not necessarily lead to the emergence of a higher individual. For an ETI to take place, Michod and colleagues propose that there must be a division of labor between germ and soma (or its equivalent in ETIs other than from uni- to multicellular organisms), since without it, the collective fitness will be proportional to the average particle fitness. As such, the collective will not be an individual with its own fitness (Michod 2005, 569); its fitness will merely be a cross level by-product of its particles’ fitness.

### *Claim 1*

As I noted earlier, Michod and colleagues define the fitness of an entity (whether particle or collective) as the product of its viability and fecundity, which is often done in life-history models. In the cases of transition from unicellular to multicellular organisms with full separation

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<sup>1</sup> The distinction between particle and collective comes from Okasha (2006, 4)

of germ and soma, if a cell does not specialize, it will invest its resources in both the viability and fecundity components of fitness. As a result its fitness will be positive. However, Michod (2005, 2011) and Okasha (2009) both generalize this argument over other ETIs and propose that:

- (1) If a particle invests everything in the somatic (or germ) function (or its equivalent) of the future collective individual, it will have a fitness equal to 0, since although its viability (or fecundity) component of fitness will be positive, its fecundity (or viability) component and consequently the product of viability and fecundity will be nil.

However, when the two types of particles combine their investment in both components of fitness (one investing everything in the soma and the other everything in the germ function) a new collective individual emerges with its own fitness. This reasoning leads Michod and colleagues to claim that during an ETI transfer of fitness from the particle to the collective level.

### *Claim 2*

Okasha (2006) and Michod (2005, 2011), mostly relying on Okasha's analysis, both link this work to the two concepts of multilevel selection distinguished by Damuth and Heisler (1988), namely MLS1 and MLS2. In the MLS1 framework, the focal unit of selection is the particle. For that reason fitness is expressed in a number of particles produced. For example, a group of particles will have a higher fitness than another if *ceteris paribus* it produces more particles. In MLS1, the fitness of the collective is merely a "by-product" of the different fitnesses of the particles composing this collective. In the MLS2 framework, the focal units of selection are both the particle and the collective. Fitnesses of the collective and of the particle are measured in different units. The fitness of a collective is expressed in number of new groups it produces

independently of the number of particles each group is composed of, while the fitness of a particle is simply expressed in number of particles it produces. During an ETI, Okasha (2006, 237-238) argues, there are three stages for which MLS1 and MLS2 are alternately more relevant to describe the selection process and propose that:

- (2) MLS1 and MLS2 are two distinct *causal processes* of selection as opposed to two conventional ways of expressing selection (2006, 59; 2011, 243). During an ETI, they represent a transition in processes of selection. Not only MLS1 and MSL2 are alternately more relevant at the different stages of an ETI, they are alternately the only way to describe accurately the process of selection.

In the first stage of an ETI, the particles of the future collective start to aggregate and cooperate. The fitness of this newly formed collective is merely the average of the particles' fitness, hence MLS1 is the relevant type of selection occurring. During the second stage, the fitness of the collective is not defined in terms of the particles any more, but is proportional to the average fitness of the particles. At that stage, although MLS2 framework can be applied, so can MLS1. There is a "grey area between MLS1 and MSL2", in Okasha's words (2006, 237). However, the collective lacks individuality, since its fitness is a cross-level byproduct of the particles' fitness. During the third stage, when the transition is complete, the fitness of the collective *cannot* be expressed as the average fitness of the particles any more. The collective is now an individual on

its own and its fitness is not proportional to the fitness of the particles; both fitnesses are now incommensurable<sup>2</sup>.

### 3. When time makes a difference

Where does the incommensurability between particle and collective fitnesses come from? To this question there is no clear answer and it is not clear how there could be one even in principle. It is in fact hard to imagine that collectives could exhibit variations in fitness, without their constitutive parts exhibiting a form of variation with consequences on their own fitness. Yet Okasha believes that such scenarios exist (Okasha 2006, 106) and that they materialize when MLS2 is the framework of choice, for MLS2 framework, he claims, fits two causally distinct processes of natural selection happening in nature (Okasha 2006, 59; 2011, 243). Recall that in MLS2 framework, the fitness of the collective can be defined as a quantity “that bears no *necessary* relation to average particle fitnesses alone” (2006, 136, my emphasis). Yet, in the same sentence Okasha surprisingly asserts that “it is *impossible* that the resulting evolutionary change could be expressed in terms of particle fitnesses alone,” Okasha (2006, 136, my emphasis). Beyond, the fact that the consequence does not follow from the premise (Okasha should have used “sometimes impossible” instead of “impossible”), I propose one important reason why we should doubt this claim in any case. I will not argue here either against the MLS2 framework itself since it is obviously mathematically true. Rather, I will argue against the claim

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<sup>2</sup> Michod and colleagues use the word ‘decoupling’ to refer to this phenomenon. By decoupling they mean that the fitness at the collective level becomes expressed in a different currency than fitness at the particle level and that it is not translatable into fitness at that level



that there is incommensurability between the particle and collective fitnesses in any real cases of evolution by natural selection. The reason I will give is based on purely methodological grounds linked to time, fitness and levels of organization and will be illustrated with one of Okasha's own example of MLS2.

In chapter 7 Okasha (2006) deals with species selection, the paradigmatic case of MLS2 in the literature on the subject, and embraces Vrba's 'acid test' (1989, 155) to detect true species selection (and more generally MLS2) from mere by-products of selection at lower levels, as in MLS1. Vrba proposes that there is true species selection when the outcome of selection at the species level cannot be explained from the perspective of the organism. One stringent way to know when this happens is to seek different directions of selection at the different levels of organization. For instance, species selection, if truly independent, could in principle counteract selection at the organism level. Vrba's test will however be inconclusive when both selection processes push in the same direction, but the most reasonable attitude to adopt in such case will be to consider that selection only really occurs at the lower level, unless one would be able to display that the force at the species level has different value from the force at the organism level. Okasha claims that one example of true species selection satisfying Vrba's test is involved in the evolution/maintenance of sexual reproduction. He asserts that asexuality is advantageous at the organism level, because of the two-fold cost of producing males (Maynard Smith 1978), but that sexuality is advantageous at the species level because it allows faster evolutionary responses to rapid changes in environmental conditions. According to this reasoning, sexual lineages would be selected via species selection as a distinct process of natural selection different from selection at the organism level which favors asexual organisms.

One fundamental principle of the scientific method in experiments is to change only one variable at a time while the other are kept unchanged or controlled. To reach this goal, if one is interested in measuring the influence of  $X$  (a drug, for instance) on a population  $P$ , the experimenter will need to control the effect of  $X$  on  $P$  with another population (let us call it  $P'$  or Control) which was not administered  $X$  but which is as similar to  $P$  as possible in all other respects. Hence, if a difference is observed between the two populations, it will *only* be attributable to  $X$  because no other variable will be different. However, if  $P$  and  $P'$  are not strictly identical in all respects but  $X$ , then any observed difference could be attributable to  $X$  *or* any of the other different variable between the two populations and which could have the same effect than  $X$ . Such variables are called confounding variables. How is that relevant to our problem of species selection and Vrba's test? Vrba's test is not a scientific experiment per se, but it shares with them the necessity to be controlled. Unless all the variables relevant to selection are strictly identical at both levels in the test, the detection of a different direction of selection at those levels could be attributed either to a different process of selection at each level *or* to any other variable with different values at each level and with some relevance to selection. Just like any scientific experiment, Vrba's test requires that only one variable at a time is changed while all the other are kept unchanged.

We noted earlier that Okasha claims that the evolution/maintenance of sexual reproduction is a true case of species selection. He justifies this assertion using Vrba's test. Because, he argues, the test shows that selection pushes in two opposite directions (i.e. sexuality at the species level and asexuality at the organism level), a process of selection ontologically different from the process of selection at the organism level, must exist at the species level. But does Okasha's comparison eliminate all possible confounding variables, which would render his conclusion

spurious? In other words, is selection at the organism level assessed in the exact same way at the species level? The answer to this question is that it is not; a confounding variable does exist.

To detect this confounding variable, let us consider two types of organisms, one asexual and one sexual, under the same selection pressures. To reproduce, sexual organisms spend energy both to look for a partner and to produce gametes during meiosis, while only half of their genes will be represented at the next generation. On the contrary, asexual organisms will be able to reproduce genetically identical offspring, without any cost from meiosis or courtship and mating. Hence if the two types of organisms are in competition, the asexual ones should quickly out-compete the sexual ones, because of the supplementary costs associated to sexual reproduction. At that point, it is thus extremely tempting to claim that the fitness of an asexual organism is higher than the fitness of a sexual organism. But, if formulated as such, this claim would be incomplete and would have to be relativized over a period of time (e.g. one generation).

Why is that? First, because the fitness of an organism cannot be directly measured as, for instance, the mass of an object can be; measures of fitness are only proxies for fitness. Second, because different proxies for fitness can lead to different answers. Hence, the information about the way fitness is measured is always relevant. In fact, the reproductive output *after one generation* of an organism represents only one proxy for its fitness among an infinite number. There is no “best” period of time over which one can measure fitness. This type of problems leads Beatty & Finsen (1989) and Sober (2002) to propose a distinction between short-term and long-term fitness. In most cases the short-term reproductive output of an entity is a good proxy for fitness to grasp the evolutionary dynamics of interest. But at other times it might be insufficient, and we will need a proxy measuring the reproductive output over a longer period of time. One famous case, proposed by Fisher (1930) on sex ratio, makes the reproductive output

two generations ahead a much better proxy for fitness than one generation. More generally, proxies of fitness over long periods of time should be preferred if one is interested in evolutionary problems involving changes in the environment, as it is the case with the evolution and maintenance of sexual reproduction. This is because long term environmental changes and their consequences on selection pressures will be invisible to a proxy for fitness based on the short term reproductive output. Yet, many evolutionary problems do not involve such changes and measuring fitness as the reproductive output over one generation is fine because the environment usually does not change or changes very little over one generation. This is the case for instance if one wants to know what phenotype is optimal in a constant environment.

The confounding variable in Okasha's comparison becomes now obvious. It is the time over which fitness is assessed, which is itself a proxy for environmental changes. At the organism level, fitness is usually measured as the reproductive output after one organism's generation. At the species level, fitness is measured as the rate of extinction or speciation over much longer periods of time, sometimes many millions of years. But commensurability necessarily exists between fitness of species and fitness of organisms. Speciation and extinction events are ultimately composed of the deaths, survivals and reproductions of organisms over many generations, since the former events supervene on the latter ones. Thus, when Okasha applies Vrba's test over the maintenance/evolution of sex, he compares the fitness of organisms over one generation at the organism level with the fitness of organisms over a much higher number of generations<sup>3</sup>. Performed as such, Vrba's test remains inconclusive. Indeed, the difference observed could be either due to two processes of selection pushing in two opposite direction or to

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<sup>3</sup> In virtue of the supervenience of speciation and extinction events at the species level on death, survival and reproduction events at the organism level

two measures of one and the same process of selection over two different periods of time, pushing in one direction over the short term and in the other over the long term. In the rest of the article, I defend the latter possibility.

To see why, let us now perform Vrba's test while controlling the period of time over which fitness is measured. Controlling time could be done in two ways: (a) by measuring fitnesses at both the species level and the organism level over one organism generation and compare them over this period of time; (b) by measuring the two fitnesses over the period time that would normally be used to measure species' fitness, that is, a period long enough to detect events of speciation or extinction. Both alternatives seem to be doomed in practice, since we are neither able to measure the fitness of species over short periods of time, nor able to measure the fitness of organisms over periods of time longer than a few generations. But if we were able to do so, we would certainly find that *ceteribus paribus* asexual organisms and asexual species have a higher short-term fitness as measured by (a) than sexual organisms and sexual species, but have a lower long-term fitness as measured by (b). The reason for that is not mysterious. Asexual organisms and asexual species on average do better when the conditions are stable (as it is usually the case over one generation) while sexual organisms and sexual species do better when new environmental conditions arise (which certainly occur over several millions of years). In other words, both selection at the organism and the species level would go in the same direction once the test is controlled for the period of time over which fitness is measured.

Thus, Okasha's claim that the evolution/maintenance of sexual reproduction occurs as a result of species selection is inexact. If we follow his reasoning using time as a constant over fitness (itself as a proxy for the stability of the environment), we predict no difference between a measure of selection made at the level of the organism and another one made at the level of the

species. The most natural implication is that these different measures represent one and the same process of natural selection, but expressed in different terms and over different periods of time.

There is no logical barrier to extending this argument to all the other cases for which MLS2 has been the framework of choice. In each case, if fitness could be determined over the same period of time or in the same constant environment at each level, what seems to be ontologically different levels of selection could in principle be unified under one and the same process. Does it mean that MLS2 framework should be abandoned and always replaced by MLS1? I claim that it should not, unless one has the full availability, at any point in time, of the selection pressures on the particles under consideration. I can only see multilevel *models* as satisfying these criteria. In any *real case*, the complete list of selection pressures will be most of the time unknown or they will be constantly changing (e.g. frequency dependent selection) making thus the particle fitnesses extremely complex to determine over long period of time. When both particle and collective fitnesses are available, and that the question at stake is about the collective, I propose that the MLS2 framework should be privileged. There are two further reasons for this choice. First, the complex task of measuring fitness of all the particles within a collective (with all the non-linear relations it implies) and over many particles' generations will often materialize at the collective level into a single and easily measurable parameter: the collective's reproductive output. Second, keeping fitness of the particles and fitness of the collectives independent, as it is done in MLS2 framework, can bring different, yet relevant, information about the selection since they are measured over different periods of time.

After these general consideration on MLS2 what does the distinction MLS1/MLS2 become in the context of ETIs and especially during their last stage? Would it be, in principle, possible, at the last stage, to describe the fitness of a collective in terms of the fitnesses of its particles,

*contra* Okasha? Following the reasoning I used in the case of the evolution/maintenance of sex, as in any case of MLS2, I see nothing that would prevent it. During an ETI, if the fitness of the particles seems incommensurable with the fitness of the collective, it is most probably due to the fact that, during the last stage, both fitnesses are not measured over the same period of time anymore and that the interactions between particles become so complex that tracking back their fitness over longer periods of time than one or two generation appears in practice impossible. What becomes decoupled in the two levels is not fitness per se but generations or life cycles. Because Michod's proxy for fitness depends on reproductive output after one generation, if "one generation" does not mean the same thing at the particle and the collective level, it is not surprising that collective and particle fitnesses seem decoupled from each other. But this is an artifact created by the measure. That does not mean that MLS2 represents an ontologically distinct process of selection from MLS1. Rather, it suggests that MLS2 is very useful means to carve one single processes of natural selection both in time and space and becomes especially useful once an ETI is completed. This echoes a recent criticism made by Waters (2011) about Okasha's fundamentalism over the distinction between MLS1/MLS2 in which he claimed that MLS1 and MSL2 frameworks were conventional rather than fundamental. Okasha (Okasha 2011, 243) held his ground, restating that they were fundamental. I have provided evidence here that they clearly were conventional and it became apparent once measures of fitness were controlled over time.

#### **4. Conclusion**

I have demonstrated that time is an extremely important parameter to take into account in regards to the concept of fitness. I argued for its relevance in ETIs and, more generally, in the levels of selection debate. I used the evolution/maintenance of sexual reproduction as a case study to establish that if different proxies of fitness reflecting different time scales are used at the organism and species levels, this will have the consequence of measuring selection pressures over two different time scales. This can lead one to confound the existence of one unique process of selection over two different periods of time with two ontologically distinct processes of selection, one for each level. I applied the same reasoning to ETIs and argued that they were not transitions in processes of selection, but rather events for which MLS1 and MLS2 were, although ultimately formally equivalent, alternately more relevant. The claim that distinction between collective selection and particle selection is conventional is not new (e.g. : Dugatkin & Reeve 1994; Sterelny 1996) and Kerr & Godfrey-Smith (2002) have formalized this equivalence. Yet, as Okasha (2006, 136) rightly points out, this formalism has been made solely in the context of MLS1. Taking time as an important variable in measures of fitness represents one important step towards a formalism in which events of selection normally described under the MLS2 framework, such as the last stage of ETIs, could also be, described under the MLS1 framework.

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