A CAUSAL DISPOSITIONAL ACCOUNT OF FITNESS

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The notion of fitness is a key concept invoked in classical evolutionary biology to explain evolutionary change: natural selection operates whenever individuals in a population differ in their fitness. Although in Darwin's original formulation what we call "fitness" referred to survival and reproductive *ability* (fitter organisms would have a better chance of surviving and reproducing), biologists today usually define fitness in terms of the *actual* number of offspring left by an individual or type. However, this actualist definition of fitness has been challenged for involving circular explanations. If we seek to explain why an organism A leaves more offspring than an organism B, the explanation "because A is fitter than B" is circular if "A is fitter than B" means "A leaves more offspring than B" (Brandon 1978; Rosenberg 1985; Millstein forthcoming).

In order to overcome such difficulties, philosophers of biology have offered alternative definitions in which fitness and reproductive success are distinguished. In the late 1970s Brandon (1978) and Mills and Beatty (1979) offered a "propensity interpretation of fitness" (hereafter PIF) as an alternative to the actualist definition. According to PIF, fitness (or "adaptedness" in Brandon's terminology) does not refer to an organism's actual survival and reproductive success, but rather to its propensity, ability or disposition to survive and reproduce in a particular environment and population. This ability is expressed in probabilistic terms, namely the reproductive success that is expected of an organism ("expected fitness"). But insofar as it is a probability, it can differ from the actual reproductive success of the organism ("realized fitness"). By distinguishing between fitness and actual reproductive success, PIF overcomes circular explanations since actual reproductive success is only an indicator of an organism's ability to reproduce: a fitter or better adapted organism has the best chance of out-surviving and out-reproducing the less fit, but it may not do so (Beatty and Finsen 1989, 17–18; Brandon and Beatty 1984).

Although I agree with this interpretation of fitness as a disposition, I disagree with respect to how this disposition should be understood (Triviño and Nuño de la Rosa in press). One of the weaknesses of the propensity interpretation of fitness (PIF) is that fitness is defined as a single disposition oriented towards the survival and reproduction of the organism. Hence, this approach leaves open the question of how the ability to survive and reproduce relates to the (ecologically relative) physical and behavioural properties of the organism. In order to solve this kind of problems that affect the propensity interpretation of fitness, I propose a new definition, inspired by Mumford and Anjum's dispositional theory of causation (hereafter DTC), in which fitness is understood as a causal dispositional property. According to this definition:

Fitness is a causal disposition resulting from the non-linear combination of environmentally relative functional dispositions oriented towards an effect (surviving and reproducing) which is reached once the combination of these dispositions exceeds a certain threshold (see Fig. 1).

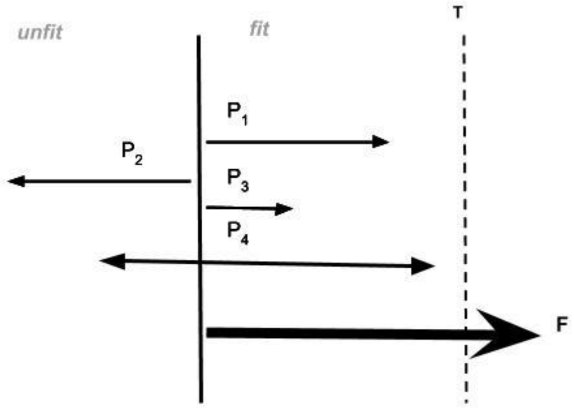

Figure 1. Fitness as a causal dispositional property. The P_n vectors refer to those dispositional properties whose combination makes an organism fit. Vectors have two properties. First, they have different intensities, as indicated by the different lengths of the arrows. Second, vectors have different directions, indicated by the direction into which the arrowhead is pointing. Functional dispositions are oriented towards (P_1 P_3, P_4) and away from (P_2) the disposition to survive and reproduce. P_4 reflects a tension in the orientation of that disposition. A sexual adaptation, for instance, can be oriented towards reproduction (arrow to the right) but be detrimental to the survival of the organism (arrow to the left). Fitness (F) is the resultant of the combination of these dispositions, and is manifested once it has exceeded a certain threshold (T).

This approach to fitness is akin to the dispositional approach to biological functions. In this view, a phenotypic trait has a function when it contributes to a higher-level capacity of the biological system it belongs to (Cummins 1975). Some authors have identified this systemic capacity with the goals of surviving and reproducing (Boorse 2002). For instance, the heart pumps blood in the circulatory system of an organism, thereby supplying nutrients and removing wastes and, in this way, it contributes to the survival of the organism. In a similar way, Bigelow and Pargetter had argued that “something has a (biological) function just when it confers a survival-enhancing propensity on the creature that possesses it” (Bigelow and Pargetter 1987, 108). The relationship between fitness and its component dispositional functions illustrate that there is not a relation of temporal priority between cause (systemic functions) and effect (fitness) as it is assumed in a classical Humean view of causation. Rather, the dispositional components that make up the fitness of an organism are simultaneous with fitness itself. A healthy organism, whose heart pumps, or whose legs run when its nose smells a predator, is simultaneously a fit organism.

One important aspect of this account of fitness is that no biological function in isolation can be directed towards the effect of surviving and reproducing. The reason is that fitness as a composite disposition involves different thresholds. Organismal functions have their own thresholds associated with their corresponding goals (see Fig. 2). Once a function reaches its own threshold, the effect associated with it is manifested. For instance, limbs are disposed to run and this disposition is manifested once the muscles and bones that make up a limb have reached a certain developmental stage and encounter an environmental circumstance that leads them to move. But the particular goals of functional dispositions, insofar as they act in composition with the other dispositions composing fitness, are subordinated to a systemic goal of the organism, namely to survive and reproduce. Hence, in this account, the overall fitness of an organism can only be reached when the *combination* of all the functional dispositions oriented towards particular systemic capacities achieves the *fitness threshold.* Thus, running is a disposition that, combined with other dispositions, such as pumping blood or seeing, is oriented towards surviving and reproducing. In this sense, individual fitness is foundational regarding trait fitness (Pence and Ramsey 2012) since the fitness of a trait can only be defined with regards to its contribution to the overall fitness of an organism. Moreover, there are actually two thresholds that need to be distinguished when talking about the fitness disposition: the *survival threshold*, which is reached whenever there is a proper combination of biological functions that allows the organism to survive, and the *reproductive threshold*, which presupposes the first threshold and is reached once the organism lives to maturity and reproduces.

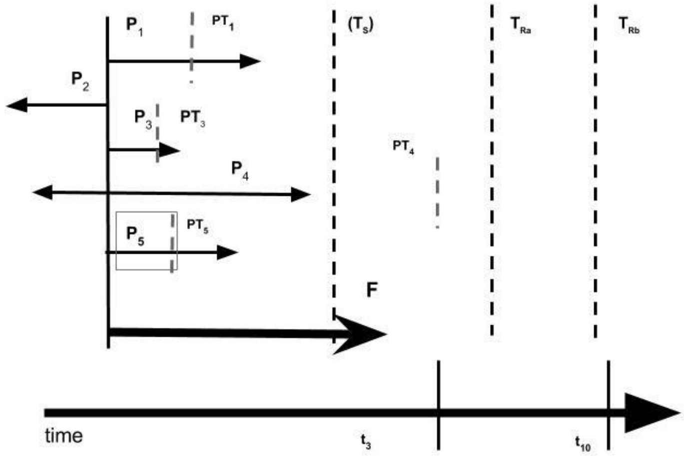

Figure 2. **Fitness thresholds.** The survival threshold (T_S) overlaps with the fitness threshold since a reproducing organism has necessarily reached the survival threshold. PT_1, PT_3, PT_4 and PT_5, refer to the thresholds of the biological functions contributing to fitness, P_1, P_2, P_3, P_4 and P_5. Notice that PT_4, the threshold associated to sexual organs, is not reached since the organism is not in its mature age yet. At t_3 and t_{10} the organism will be able to have offspring providing that fitness reaches the “reproductive threshold” ($T_{Ra,b}$). At t_{10}, when the organism gets old and becomes infertile, the sexual traits do not reach their own threshold (PT_4) and therefore, the R_T can no longer be reached.

DTC allows to disentangle the complexity of fitness by considering the ***direction*** and ***intensity*** of the dispositions composing this complex disposition. Regarding the *direction* of dispositions, I have endorsed a dispositional notion of fitness according to which dispositions are combined and oriented towards the effect of surviving and reproducing. Nonetheless, this approach does not mean that every functional trait of an organism necessarily contributes in a positive way to its fitness. As the proponents of the DTC have noticed, there are powers that dispose away from reaching a given threshold (see Fig. 1, P_2). This is the case of maladaptive functions such as those resulting from the disrupting effects of a malformed or a sick organ. Well-formed and healthy traits may also prove to be maladaptive in a given environment. Furthermore, I argue that the case of fitness shows that there are also powers that can dispose *both towards and away from* the threshold. In particular, sexual characteristics can prove to be a hindrance to an organism insofar as they might be oriented towards the goal of reproduction but also against the goal of surviving (see Fig. 1, P_4). A well-known example in evolutionary biology is the bright coloration of many male birds, which, in addition to attracting females (thus contributing to the goal of reproduction), also calls the attention of predators (thus being detrimental for the goal of surviving).

Regarding the *intensity* of dispositions, while all living organisms have reached the survival threshold insofar as they are alive, fitness varies in intensity depending on the populational and environmental context of the organism. Nonetheless, “viability constraints” define the limits within which the organism can continue alive and reach the “survival threshold”. Each dispositional function has its own viability constraints (for instance, the human heart cannot beat at more than 180 beats per minute) and they vary depending on the organismal and environmental context. The same happens with regard to the reproductive threshold. Once the organism is in its mature stage, the organism’s disposition to reproduce is able to reach its own threshold, i.e. having offspring. When the sexual organs do not longer fulfil their own tasks, i.e. once the intensity by which the biological function of sexual traits is manifested decreases and does not reach its own threshold, the disposition to reproduce cannot reach the reproductive threshold and have its full effect (i.e. having offspring).

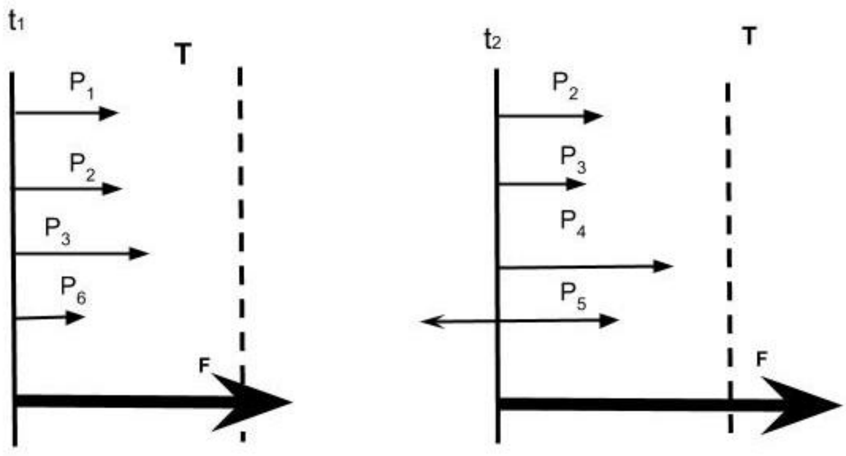

Figure 3. The development of fitness. Each vector diagram represents a causal situation at a particular time (two different developmental stages, t_1 and t_2) and includes those powers that are causally relevant for the fitness of the same organism. Figure t_1 represents fitness in an embryo. Figure t_2 represents fitness in an adult. The functional dispositions that give rise to fitness change along the life history of an organism: P_1 and P_6 are traits that embryos have but not adults, while P_4 and P_5 are traits (e.g. sexual traits) that only mature organisms have.

However, fitness does not only change as a result of the changing intensities of the dispositions composing it at a particular stage of the life cycle. One of the difficulties of characterising biological dispositions derives from the radically dynamical character of biological organisation. The morphological, physiological, and behavioral properties of an organism are not static but change along the life history of the organism (see Fig. 3). The functional dispositions that make an embryo fit are not the same as those that make an adult fit. Some traits are essential for the survival of an embryo (e.g. the chorion, or the fetal part of the placenta in mammals) whereas some traits that are not present at the embryo stage (e.g. some sexual traits) will become vital for the survival and reproduction of an adult. The resultant fitness evolves throughout the development of the organism, and, in this sense, fitness should be considered as "a property of the organism's life history", rather than as an "instantaneous property" (Brandon 2005, 166).

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