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Fitness, Reproductive Success and Functions

Abstract

The notion of fitness has traditionally played two roles in evolutionary biology: As an *ecological descriptor* and as a *mathematical predictor* (Sober [2001]). The orthodox notion of fitness fails to account for the role of the notion as an ecological descriptor. The propensity interpretation of fitness (PIF) aims at explaining the reproductive success of organisms by relying on the notion of disposition. If successful, it can account for the organism-environment relation through the stimulus conditions for the disposition to reproduce successfully, hence fulfilling the role of ecological descriptor. In this paper I will show that the PIF fails to do so. In order to fulfill the role of ecological descriptor, a new approach is needed.

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1 Introduction

Fitness is a central notion that has traditionally played *two roles* in evolutionary biology and ecology (Sober [2001]). On the one hand, it has functioned as an 'ecological descriptor' (Sober [2001], p.26). Descriptions of the respects in which an organism 'fits' to its environment include descriptions of certain organism-environment-relations which enable survival and/or reproduction of the organism and/or its offspring. On the other hand, the notion of fitness plays predictive or explanatory roles, referred to by Sober as 'mathematical predictor' ([2001], p. 26). For example, the difference in the fitness of certain organisms in a population can explain the difference in the distribution of different trait of those organisms in that population.

Although each of these roles has been investigated separately in different evolutionary contexts, the relation between them has been vastly ignored.[1] Are these roles indicators of two different notions that are mistaken to be one single concept or are they merely two roles of one notion? If the latter were true, then one might assume that descriptions of the organism-environment relations that contribute to the survival or reproduction of organisms in a population (first role) were part of the explanations that use this notion (second role). As intuitive as this might sound, it is debatable how the explanatory role could be fulfilled at all if we took the traditional definition of fitness into account. For example, one of the main concerns about the explanatory power of the notion of fitness has been that if fitness were understood in terms of the actual reproductive success, as it traditionally has been (*Inter alia*: Zrzavý, Burda, Storch, Begall and Mihulka [2009] p. 12 & 462 and Ridley [2004] p. 74 & 684), then one could argue that it could not be used to explain the difference in the distribution of different trait types in a population, for then the explanation would be circular. This is the so-called tautology problem: roughly put, if the notion of fitness is defined in terms of actual evolutionary

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[1] Ariew and Lewontin [2004] are among the few who have actually investigated this relation and confusions surrounding it. Their conclusion in this regard is in line with mine in this paper. However, my explanatory purposes deviate from and go beyond theirs.

outcomes, then it cannot be used to explain those very outcomes. On the other hand, if we had two (or more) different notions that were mistaken to be one concept, we need to sharpen and clarify the different notions, their relations and their explanatory significances. This is important not only to have better understanding of these notions and their relations to each other but to have better grasp of their applications.

Against this background, one of my goals in this paper is to clarify the above described dichotomy. My first step is to take what seems to be the most common understandings of fitness in evolutionary biology (let us call this *the orthodox notion*) as a starting point and see what this notion can and cannot explain or predict. This will help us sort out some of the controversies surrounding the explanatory and predictive power of this notion. I will conclude that the orthodox notion is primarily concerned with evolutionary outcomes and at the end of Section 2 I will show that even though the orthodox notion has some predictive values it does not address the organism-environment relation. If a description of such relation is being provided, it is not by the orthodox notion. This outcome suggests that the illustrated two roles are probably being played by two different notions (given that the predictive role that the orthodox notion plays is one of the predictive roles that is being ascribed the notion of fitness.). Assuming this is true, an investigation into other notions that might fulfill the first role (as ecological descriptor) is much needed. One of the most suitable candidates to consider is the so-called propensity interpretation of fitness (or the PIF)[2], which aims to explain differences or changes in the distribution of trait types within a population by relying on dispositions. The propensity theory is worth considering, because if it is successful in achieving its explanatory goals, it has the theoretical resources to fulfill the first role: Descriptions of stimulus conditions of manifestation of the disposition to reproduce successfully would include descriptions of specific organism-environment relations that result in reproductive success, which is precisely what the first role was about. After showing the motives and merits of the PIF in Section 3, I will, however, argue in Section 4 that this theory cannot achieve the explanatory goals that it sets for itself and ergo fails to serve the role of ecological descriptor. I will identify three independent problems with the propensity notion.

In Section 5 I will propose a new approach to explain the *explananda* of the PIF. The new approach does not have the problems that the PIF is encountered with. I will argue that this

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[2] I will refer to the PIF as a theory rather than an interpretation, for it is less like an interpretation of already existing notion and more like developing a notion for specific explanatory purposes. But this is just a terminological preference and does not have any theoretical importance.

approach can provide us with descriptions of the organism-environment relations that are included in explanations of reproductive success of organisms involved.

2 Fitness as the reproductive success: The orthodox notions

The orthodox notion of fitness in biological textbooks is usually defined as relative reproductive success of an organism or the actual (or sometimes the average) number of offspring it produces (Cf. Zrzavý, Burda, Storch, Begall and Mihulka [2009], p. 12 & 462 and Ridley [2004], p. 74 & 684). The orthodox notion of fitness takes at least three main forms. In its most general form, the fitness of an organism or a genotype is defined in terms of the organism's or the genotype's contribution to the gene pool of the population in the next generation. The disjunction "an organism or a genotype" marks different explanatory interests in different subdisciplines in biology, such as molecular genetics, population genetics, developmental biology, behavioral biology and ecology. Let us retain this definition in a canonical form in order to track the changes in the other two forms:

> (OF) The fitness of an organism or a genotype is its contribution to the gene pool of the population in the next generation.

In a slightly less general form, the contribution is understood or defined as *the reproductive success* of the organism (or the genotype). The second form then of the orthodox notion could be formulated as following:

> (OF*) The fitness of an organism or a genotype is its reproductive success.

The question here is, what is the reproductive success of an organism or a genotype? One of the least controversial and most widely accepted measurements of reproductive success is in terms of the number of offspring produced by the organism or the genotype. Thus, replacing this measurement in (OF*) yields the third form as following:

> (OF**) The fitness of an organism is measured by the total number of offspring produced by the organism or genotype.

I reconstructed the relation between different forms of the orthodox notion of fitness in this three-step manner for two reasons. Firstly, the second (OF*) and third (OF**) forms could be seen as operationalizations rather than reformulations or explications of (OF). Secondly, this approach helps us to see the levels of generality of each notion and how these different notions of fitness are interrelated.

As I have stated, my first aim is to explore the explanatory and predictive power of the orthodox notion. For now, let us focus on (OF**), for it is the most applicable form of the

orthodox notion by giving us a value for fitness. A fitness value of a single organism is useful only in comparison to fitness of other individuals. One of the most efficient ways of having meaningful comparisons is to divide this number by the number of offspring of the reproductively most successful individual of the same type in the population[3]. This gives us the *relative fitness* of an organism, which allows us to compare fitness of organisms of the same type or different types within a certain population (or between organisms in different populations) in a scientifically meaningful way.

Remember that we are still on the level of individuals: the relative fitness of an organism *a* is higher or lower than the relative fitness of an organism *b*. What does this difference in relative fitness imply? What is the theoretical importance of this assessment? Whether or not a difference in relative fitness is of any significance for the evolutionary theory depends on two factors. First, it depends on the criteria by which we classify the organisms into types. Note that we could build infinite numbers of biologically *non-relevant* classes, such as all the organisms in the population that John loves; hence it matters how we distinguish different types. Second, the evolutionary significance of a difference in relative fitness depends on how representative the relative fitness of the organisms is for their particular types. The relative fitness difference of two organisms of different types may be a happy accident or it may be caused in a principled way. The former has little theoretical value; the latter could be used for meaningful generalizations.

One of the most conventional ways of overcoming the first difficulty is to classify groups of organisms by *specific types of traits* in a certain population. And in order to have a better representation of the reproductive success of a certain type of organisms, one can estimate the average relative fitness of the group. Applying this, a difference in the average relative fitness of two groups of organisms would mean that the average reproductive success of organisms with a specific type of trait in a specific population is higher than that of organisms with another type of trait in that population. This is of course nothing other than the *selection of* that type of trait, which is of significance for evolutionary biology. The predictive value of this is quite obvious: if everything stays the same, we would expect organisms classified by a specific type of trait T_1 and have a higher average reproductive success than those classified by another type of trait T_2 to reproduce on average more successfully; and we would also expect that the average difference in the number of offspring of T_1-organisms and T_2-organisms remains approximately the same as previously estimated. Think of a coin that has been tossed 5000 times and the result

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[3] I do not intend to define a population in a certain way here. However, I presuppose that a population could consist of individuals of different types – however these types might be defined.

was 80% heads and 20% tails. If we were to toss the same coin for another 100 times under the same or similar conditions, we would expect there to be more heads than tails and that the average relation between them stays approximately 4:1. This has predictive value and is scientifically applicable.

However, the explanatory or predictive significance of (relative average) fitness comparison with the above suggested classifications (through trait types) does not extend beyond the *mere correlation* between certain trait types and the reproductive success of organisms that have those traits. A difference in fitness between organisms with different types of traits says nothing about the *causal role* of those traits in achieving the fitness difference. And this is the explanatory limit of the orthodox accounts of fitness. This is not to deny that the correlation between trait types and fitness could have explanatory or predictive value for biologists; as we established, it can have such value. Instead, what is implied is that, if one is interested in the question of why there is a difference in distribution of certain trait types in a certain population, then the orthodox notion of fitness does not answer the question (but rather confirms the premise of the question).

Furthermore, notice that the orthodox notion of fitness does not say anything about the relation between organisms and their environment and in particular whether this relation is one of 'fit'. The orthodox notion is focused on evolutionary outcomes and not on how these outcomes are achieved. Therefore, if we take the orthodox notion into account, the role of fitness as an ecological descriptor requires another distinct notion. As I laid out in the last Section, the PIF has the theoretical resources to fulfill this role by relying on the notion of disposition. However, the fulfillment of this theoretical feat is dependent on capacity of the PIF to explain the reproductive success of organisms or disparity in distribution of trait types in a population through the notion of disposition. How or if this is the case, I will discuss in the next two Sections.

3 The propensity interpretation of fitness

3.1 Motivation

Mills and Beatty (M&B), some of the first developers of the PIF (alongside Brandon [1978, 1990] and Popper [1978]), claimed to have identified at least two major problems with the orthodox notion of fitness. The first problem was that there are certain explanations which would be flagrantly circular if we were to define fitness differences in terms of reproductive success of two types of organism distinguished through different trait types:

> The explanations in question are those which point to fitness differences between alternate types in a population in order to account for (1) differences in the average offspring contributions of those phenotypes, and (2) changes in the proportions of the types over time (i.e., evolutionary changes). (Mills and Beatty [1979], p. 5)

As illustrated in the last section, we cannot causally explain the difference in distribution of trait types in a population by referring to the orthodox notion of fitness. However, it is not clear whether or not biologists use the orthodox notion to explain the *explananda* identified by M&B ((1) and (2)). M&B name only one example of such a usage (Namely: "Kettlewell (1955, 1956)" Mills and Beatty [1979], p. 5). Nevertheless, my aim is neither to defend biologists nor to show their (alleged) mistakes in certain usages of the term "fitness" in their explanations. My goal is to point out the explanatory limits of the orthodox notion and try to specify a respect in which the organism-environment relation principally explains the evolutionary outcomes that the orthodox notion captures, thereby clarifying the relation between "two faces of fitness". M&B's second problem with the orthodox notion concerns, generally speaking, a conflict between biologists' usage of the term "fitness" and theoretical feats of the orthodox notion, which, as clarified, will not fall under the scope of explanatory goals of this paper.[4]

One last remark before I start to reconstruct M&B's notion of fitness. It is important to point out what their theory is supposed to achieve. They are, as we will see, quite clear about the fact that the orthodox notion does not deliver causal explanations of (1) and (2) and also about the fact that their theory is supposed to deliver a causal explanation of (1) and (2). Such an explanation, if it explains (1) and (2) in general (i.e., in a principled way), would solve what Pence and Ramsey call *the generality problem* (Pence and Ramsey [2013], p. 853). The generality problem is, roughly speaking, the difficulty to find a *general explanation* of evolutionary outcomes such as the selection of trait types in a population. Their understanding of a general explanation of evolutionary outcomes covers explanations that "do not focus on particular episodes of natural selection, but rather on what it is that is common to every instance of natural selection, across every environment […] where natural selection might be instantiated." (Pence and Ramsey [2013], p. 853) The PIF claims to deliver such an explanation by relying on dispositions. But what kind of dispositions? Disposition to do what exactly? And how do they explain evolutionary outcomes/changes?

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[4] Biologists tend to, M&B assume, ascribe the same or similar fitness values to organisms that are genetically and phenotypically identical, and inhabit the same environment. Yet the orthodox notion would ascribe drastically different fitness value to such organisms if one of them happened to have an unlucky accident and die before it could reproduce while the other organism was able to reproduce successfully (Cf. Mills and Beatty (1979), p. 7).

3.2 The Theory

According to the PIF, the fitness of an organism is, roughly speaking, its propensity to survive and reproduce in a certain environment and population (Cf. Mills & Beatty [1979], p. 9). Before clarifying the concept of propensity that M&B use, let us formulate this crude definition in a canonical way. As I will discuss later in Section 4.2, M&B's canonical formulation of the PIF deviates from this formulation.

> (C-PIF) The fitness of an organism is its propensity to reproduce[5] in a certain environment.

What do M&B mean with "propensity"? Their usage of the term goes back to Popper's "The propensity interpretation of probability."(Popper [1959]) "Propensity" usually denote a stochastic disposition. Nevertheless, M&B seem to use the terms "propensity" and "disposition" interchangeably (see the second quote below). To avoid unnecessary complications, I will treat the two terms as synonym.[6]

Now, let us consider some implications of (C-PIF) for explanations of (1) and (2). M&B consider an analogous case to show the explanatory significance of defining fitness in terms of dispositions:

> The fitness of an organism explains its success at survival and reproduction in a particular environment in the same way that the solubility of a substance explains the fact that it has dissolved in a particular liquid. (Mills & Beatty [1979], p. 9)

In this analogy they refer to physical properties of salt as the explanatory aspects that causally explain why salt has the disposition to dissolve in water:

> When we say that an entity has a propensity (disposition, tendency, capability) to behave in a particular way, we mean that certain physical properties of the entity determine, or are causally relevant to, the particular behavior whenever the entity is subjected to appropriate "triggering conditions." For instance, the propensity of salt to dissolve in water (the "water solubility" of salt) consists in (i.e., "water solubility" refers to) its ionic crystalline character, which causes salt to dissolve whenever the appropriate triggering condition—immersion in water—is met. (Mills & Beatty [1979], p. 9)

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[5] M&B clarify later what they understand under "propensity to reproduce": "the property of organisms which is of interest to the evolutionary biologist is not the organism's propensity to reproduce or not to reproduce, but rather the quantity of offspring which the organism has the propensity to contribute." (p. 10) However, this clarification is one step into operationalization of the propensity notion.

[6] Drouet and Merlin, in accordance with Popper, suggest that propensities are certain kind of dispositions, namely "stochastic dispositions that get manifested only with a certain probability, even when the triggering conditions are present and the disturbing factors are absent." Drouet & Merlin [2015], p. 461. Propensities are contrasted with so called *deterministic dispositions* which get manifested with the probability of 1 when the triggering conditions are present and the disturbing factors are absent. However, this difference is of little importance for my explanatory purposes and I will ignore it in this paper.

They argue by analogy that "the fitness of an organism consists in its having traits which condition its production of offspring in a given environment." (Mills & Beatty [1979], p. 9) In other words, if one asks why there are differences in the average offspring contributions between organisms with alternate trait types, the answer would refer to certain physical properties which cause the organisms, given a certain environment, to reproduce successfully. So, we get the following general schema of dispositional properties from M&B's analogy:

(DSP) x has the disposition to do y if C if

1) x has the set of physical properties $s = \{p_1,\ldots, p_n\}$ and

2) (certain stimulus conditions) C is such that s is sufficient to cause y if C (is met).

The PIF claims that by referring to fitness one refers (implicitly) to a set of physical properties that cause the effect of reproductive success. Hence, the PIF allows one to causally explain reproductive success.

But how do we identify the relevant set properties and the stimulus conditions under which these properties cause the productive success of the focal organisms? These properties are certainly not just any physical properties and, as Pence and Ramsey correctly argued:

> It's clear that not just any physical difference, or even any physical difference that's causally connected to survival and reproduction, will suffice for being counted as taking part in selection. Each individual mammal, for example, has a unique pattern of hair follicles, and if hair is causally relevant to survival in some species, then *a fortiori* the pattern of individual hairs is as well. But it does not therefore follow that there is a selective difference between each pair of individuals that is due to their follicle pattern difference. We thus need some way to cash out selection in terms of relevant physical differences between organisms. (Pence and Ramsey [2013], p. 855)

And a similar argument can be formulated for the stimulus conditions. These are not just any environmental conditions that are present when the reproductive success is achieved. So again: How do we identify the stimulus conditions? Or: What connects specific stimulus conditions to a specific disposition (here i.e. to reproduce successfully)?

Before trying to answer the above questions in the next Sections, let us briefly consider the theoretical significance of answering them for the PIF. Can the PIF get away with not answering these questions? In other words: Would not-identifying the relevant set of properties and the stimulus conditions strip away the explanatory power of the PIF? The answer is that the PIF would still have some explanatory values. Explaining the reproductive success in terms of a disposition to reproduce successfully without identifying the (above clarified) relevant properties and conditions is analogous to Dr. Pangloss's explanation that a drug makes someone

fall asleep because it possesses a *dormative virtue* (a sleep-producing effect)[7]. This explanation, as circular as it might sound, is not empty, for the sleeping effect could have been caused in alternate ways, for instance one falls asleep because one was exhausted. Therefore, depending on one's explanatory goals, this explanation can have epistemic value. However, if one is interested in explanations that is analogous to the explanation of solubility of salt in water by referring to ionic crystalline character of salt, as M&B and biologists in large do, then referring to dormative virtue of the drug in question is insufficient. More precisely, one needs then to refer to the chemical structure of the drug and conditions under which such structure leads to the sleeping effect in the organisms that take the drug. Therefore, identifying the relevant physical properties and conditions under which such properties cause the realization of the propensity to reproduce successfully would turn a mere explanation of the dormative virtue type to a substantial explanation with a more detailed description of the relevant causes. Furthermore, identifying the relevant stimulus conditions would help us in our quest to find a description of an organism-environment relation that explains the reproductive success of focal organisms and thereby finding a candidate to fulfill the first role of the notion of fitness.

In the following Section (3.3) I will investigate the connection between the stimulus conditions and dispositions. After arguing (in Section 4) that such connection does not work for the disposition to reproduce successfully, in Section 5 I will introduce a way to identify the relevant properties and conditions under which these properties cause the reproductive success.

3.3 Linking Dispositions and Conditionals

Now, how do we determine the stimulus conditions for a certain disposition? What links stimulus conditions to dispositions? It could not be merely that something has a disposition to do a certain thing in a certain condition if and only if it would do it if the condition were met, for it could be 'forced' to do the job by an *external* device under that condition. This is the so-called *problem of finks* (See: Martin [1994] and Lewis [1997]).[8] In order to dispose of this problem, Lewis suggest the following definition:

> Something *x* is disposed at time *t* to give response *r* to stimulus *s*, iff, for some intrinsic property *B* that *x* has at *t*, for some time *t*' after *t*, if *x* were to undergo stimulus *s* at time t and retain property *B* until *t*', *s* and *x*'s having of *B* would jointly be an *x*-complete cause of *x*'s giving response *r*. (Lewis [1997], p. 149)

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[7] This analogy (which since has come to be known as "explanations of the dormative virtue type") was introduced by Godfrey-Smith [1996] in his argument against entirely output-oriented teleosemantics.

[8] In addition to the problem of finks, this understanding of disposition has the so-called *problem of revers finks* which suggest that something could have the intrinsic disposition to do a certain thing but removed of its disposition by an external device and therefore do not manifest its disposition under the stimulus conditions. For a systematic reconstruction of discussions on dispositions and conditionals see: Manley and Wasserman [2008].

Roughly speaking, Lewis tries to solve the problem of finks by ensuring that some intrinsic properties of the entity with the disposition were responsible for the manifestation of the disposition in question and it was not forced. Notice that my interpretation of M&B's understanding of dispositions (DSP) is close to Lewis' account.

Although this account gets rid of the problem of finks, it is still vulnerable *inter alia* to the *problem of masks* (See: Johnson [1992]).[9] In short, the problem of masks is that the manifestation of a disposition can be hindered even if the stimulus conditions are met and the underlying causal basis or intrinsic properties of the object in question are intact. For example, if we put salt into a saturated brine, it would not dissolve. M&B wave away these problems by assuming that the stimulus conditions C would cause y in the presence of s and 'the absence of disturbing factors.' (Mills & Beatty [1979], p. 9) But this response calls for an account of what makes something a *disturbing* factor. A convenient way of solving this problem is to get specific about the stimulus conditions, so that the disturbing factors would be excluded. However, getting specific brings about other problems such as *Achilles' heel* cases. Think of a glass that would break only if it is dropped at a very specific angle and hits the floor on a very specific point at a very specific speed and so on, and otherwise would not break. We would not say that the glass has a disposition to break if dropped, although there is a very specific stimulus condition under which it would break if it is dropped (Cf. Manley and Wasserman [2008], p. 67ff).

Without going any deeper into problems of linking dispositions and conditionals let us consider a proposal from Manley and Wasserman to solve these problems. My goal here though is not to defend one particular theory of dispositions that solves all the problems mentioned above. My aim is rather to get an example of how these problems can be handled and try to capture aspects of that answer that could be true in general and then see if that could bring us closer to identifying stimulus conditions of the manifestation of the disposition to reproduce successfully.

The Achilles' heel problem raises the question of connection between ordinary dispositions and highly specific ones. Manley and Wasserman suggest that we may require not all of the conditions in a highly specific disposition, but rather many or most of them. For instance, for our example of the disposition of the glass N to break if dropped, we could say:

> (D) Most heights over half a meter are such that, if N were dropped from them, N would break. (Manley and Wasserman [2008], p. 74)

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[9] Of course, where there is the problem of masks there is a problem of *revers masks* (or mimicking) as well. For more discussion in this matter see also Manley and Wasserman [2008], p. 62ff.

In order to expand the account beyond height, they introduce the term 'stimulus condition case' or 'C-case' for a case of fairly specific stimulus condition containing precise combination of values for various variables (such as heights, Shore measurements, densities of the medium etc.). This brings Manley and Wasserman to the following more general definition:

> (MOST) N is disposed to M when C if and only if N would M in most C-cases.(Manley and Wasserman [2008], p. 75)[10]

Note that C-cases build an interval (or a set) of stimulus conditions, where the disposition would be most likely manifested within a range along this interval.

Let us now turn our focus slightly away from the details of this account and look at the connection between conditionals and dispositions in a more abstract way. The idea is that in order for something to have a disposition to do a certain job under certain interval of conditions, it should do it at an *appropriate frequency[11]* under this range of fairly specific conditions. If something does not do a certain thing under most of the *C*-cases, but under some really rare and specific *C*-cases, it does not have the disposition to do the thing (it has rather an Achilles' heel). Thus, to answer our initial question, what links certain stimulus conditions to a disposition is (in addition to the causal link between physical basis and the manifestation of disposition), roughly speaking, that the disposition is manifested at an appropriate frequency under this fairly specific range of conditions.

4 Remediating the PIF

Now that we have some idea about the connection between the stimulus conditions and dispositions, let us see how the PIF would identify the stimulus conditions for the disposition to reproduce successfully. Applying our finding about such connection for the analog case of solubility of salt, the identification of the set of relevant physical properties and of the corresponding stimulus conditions are pretty straightforward: these are the physical properties of salt, in particular its ionic crystalline character, that, under a range of C-cases, which consist of a certain range of temperature, density, and so on of the liquid would most frequently cause the dissolving of salt if submerged in the liquid.

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[10] It is important to remark that (MOST) is not the end-form of their account. They develop their account further, in order to get rid of some other counter examples and problems which are not relevant for my explanatory purposes here.

[11] Of course "manifestation at an *appropriate frequency* under a range of C-cases" is weaker than "manifestation in *most of the C-cases*". However, the weak formulation is in line with Manley and Wasserman's further improvement of (MOST) which is a more liberal account of dispositions.

4.1 Applicability to reproductive success

The question is now, whether or not the solubility-analogy goes through. What are the specific (ranges of) stimulus conditions for the disposition of an organism to reproduce successfully?

It is important to note that we cannot treat this disposition as a *decomposable* disposition, for then almost every condition under which an organism lives would count as a stimulus condition and then we would have the following problem. On the one hand, the stimulus conditions for manifestation of this decomposable disposition would be too specific, such that no two organisms would have the same stimulus conditions for their reproductive success. In other words, the stimulus conditions would become Achilles' heel and disqualify reproductive success as a manifestation of a disposition. On the other hand, any attempt to formulate less specific and more general the stimulus conditions would probably not go beyond the basic conditions under which the focal organisms would generally survive, for instance including the amount of oxygen the organisms would need to not die etc. Less general conditions would probably not be true for all the organisms in the population. In this case identifying these general stimulus conditions would not add sufficient epistemic value to the dormative virtue type explanation of the reproductive success.

Therefore, let us assume that the disposition to achieve reproductive success is a *complex/composable* disposition which is composed of a set of dispositions, each of which could be a complex disposition itself being composed of other sub-dispositions, and so on. For example, the disposition to reproduce successfully could consist of dispositions to catch prey, to eat, to mate etc., and the disposition to catch prey could consist of dispositions to hide and wait, to run, to attack and so on. Consequently, we end up with a set of irreducible dispositions, the sum of which builds the complex disposition to reproduce successfully.

I have three independent arguments against this account.

4.1.1 Argument 1: Indefinite set stimulus conditions

My first argument against this account is that there is no definite set of stimulus conditions for the disposition to reproductive success. To be precise, the set of (irreducible) dispositions from above is infinite, for organisms regularly develop new ways of doing the same thing under different conditions through learning, accidents, mutation, and other plastic physiological adjustments, thereby adding new dispositions to the set. If the set of sub-dispositions building the disposition to reproductive success is infinite, then the stimulus conditions causing its manifestation is undetermined.

The objection is not that the stimulus conditions contain infinite C-cases. This could be the case even for the simple disposition of the glass to break if dropped; as mentioned before, the

C-cases could include all the heights over half a meter, which would result in potentially infinite C-cases. The difference is that in this case the range of C-cases is determinate whereas in case of the complex disposition to reproduce successfully the ranges of C-cases are indefinite, for with each new disposition a new range is added to the set.

One way to react to this argument is to bite the bullet and accept that the set of stimulus conditions would be theoretically indefinite but dismiss this fact as being problematic for identifying the relevant stimulus conditions in practice. One could argue that it might be true that organisms learn to do things differently and under different conditions and it might also be true that the new ways of doing things by focal organisms are potentially infinite. However, most of organisms of certain species in a certain population possess a fairly clear set of ways of doing things and mostly limited and comprehensible learning abilities, so that in practice the set of stimulus conditions is finite (although theoretically is not). My answer to this counter-argument is less sweeping, especially because this argument bites the bullet and accept my objection. My only remark in this regard is that my objection indicates a theoretical deficit in the analysis of reproductive success in terms of dispositions and if an alternative approach lacks this deficit, then it is preferable.

4.1.2 Argument 2: Belonging to the set

Nevertheless, let us assume that the disposition to reproduce successfully consists of a finite set of sub-dispositions. The question is which dispositions of the organism are elements of this set. Certainly, not every disposition of the organism is part of the set. Not even every disposition that actually contributes to its reproductive success can be included, because then any disposition that accidently contributes to the reproductive success would be part of the set. For instance, the disposition of a deer to slip on ice would be a member of the set if it would accidently cause the deer's survival by allowing it to dodge a hunter's bullet.

An attempt to exclude such cases could be to include only dispositions that contribute to reproductive success more frequently or with an appropriate frequency. However, this approach excludes too much. Think, for instance, of the disposition to vomit when eating something poisonous. This disposition could save an organism's life even if it is only manifested once in a lifetime. Every species has accumulated throughout its evolutionary history many such lifesaving but rarely manifested dispositions. Excluding them from the set because of their seldom occurrence seems to undercut their evolutionary importance and retention.

Notice that the theory excludes these cases and the earlier cases of survival by accident for the same reason. These are the Achilles' heel cases of the set and the theory has no way of

differentiating them, even though one group should be part of the set and the other should be excluded.

Another way to oppose my argument is to rely on the 'possible worlds analysis' of dispositions. In light of such analysis, one could argue that the (possible) world in which, say, dodging a hunter's bullet by slipping on ice does not save the deer's life is closer to the actual world than the world in which vomiting reflex does not save the organism's life. In other words, if a disposition contributes to the reproduction of an organism by a freaking accident, it would not do so in the next nearest possible world, whereas if the contribution is not accidental, then it would also do so in the next nearest possible world. It seems that this analysis can differentiate between survival by accident and evolutionary relevant cases like survival by vomiting reflex. I think that this counter-argument is not as straightforward as it seems at the first glance. Let us take a more precise look at what exactly accomplish this differentiation feat. It is though the assumption that some possible worlds are nearer to the actual world than the others. Without refuting this assumption, let us see what makes it the case that some worlds are nearer to the actual world that the other in these particular examples. What is the criteria of the nearness to the actual world here? The analysis is not explicit in this regard and plays on our intuitions. However, it seems to me that any attempt to explicate the intuition would leave the frameworks of the dispositional theory. For instance, one could argue that the world in which dodging a hunter's bullet by slipping on ice does not save the deer's life is closer to the actual world than the world in which vomiting reflex does not save the organism's life, because vomiting reflex save organisms' lives *systematically* or it *supposed to* save organisms' lives etc. But then one is obligated to unpack the 'systematicity' or 'supposed to' without referring to dispositions which, I assume, would exceed the frameworks of the dispositional theory.

4.1.3 Argument 3: The linkage between stimulus conditions and dispositions

My last argument against this account concerns the way that stimulus conditions and dispositions are linked. As we established, what links them in general is the appropriate frequency by which the disposition is manifested when stimulus conditions are met.

Let us now take a look at one specific sub-disposition in a set of dispositions for the reproductive success of a predator, namely its disposition to catch prey. Let us assume that a certain predator exhibits prey-catching behaviors several times a day but is successful only once every two weeks (or three weeks or four weeks etc.). It is rarely successful with respect to the number of times it actually tries. The frequency by which it succeeds does not link the behavior to the stimulus conditions. Thus, it does not have the disposition to catch prey, even though catching prey is indispensable for its survival and hence its successful reproduction.

One might object that all the cases in which the organism tries to catch a prey and fails are not the *real stimulus conditions*. But then what are the real stimulus conditions? Defining the real stimulus conditions as conditions under which something *infallibly* manifests its disposition would return us to the highly specific stimulus condition that is Achilles' heel for the prey-catching behavior which again disqualifies the behavior as dispositional.

Another way to counter my argument is to claim that biological entities generally does not have any Achilles' heel case and depending on the species and the population a success rate of even 1% is an appropriate frequency for some dispositions. My problem with this counter-argument is that there is no non-arbitrary way of assessing the frequency percentage that links a disposition to behave in a certain way to specific stimulus conditions, as opposed to some random things that an organism very rarely under some random but similar conditions does. Consider, for example, an organism o that randomly takes a certain road on its daily scouting. In a particular month it has taken the road, say, 10 times. Now imagine that this month was especially hard for o with respect to finding prey animals and the animal was on the edge of starving when it accidently found some food on this particular road and survived because of it. To take this thought experiment one step further, imagine that the described scenario repeats in five consecutive months. What makes the prey-catching behavior from the last example a disposition and the random behavior of o to take a certain road not? If one is then inclined to bring other criteria like 'systematicity' by which one behavior occurs or something similar in play, then one is obligated to unpack such criterion without referring to dispositions, frequency or reproductive success.

In Section 5 I will introduce an approach to solve all the three problems at once.

4.2 Two faces of the PIF

As I mentioned earlier (in Section 3.2), M&B's definition of the PIF deviates from their initial account (C-PIF). Before I start with my proposal to solve the problems above, I want to briefly consider this disparity and how it comes about and why it is worth inquiring.

Having analyzed dispositions or propensities in causal manner, M&B's want to take into account that propensities to reproduce a certain number of offspring are stochastic dispositions and that this affects fitness values:

> If we could assume that there were a unique number of offspring which any organism is determined to produce […], then the $fitness_1$ of an organism could be valued simply as the number of offspring which that organism is disposed to produce. But since it is quite possible that organisms may have a range or distribution of reproductive propensities […] we derive $fitness_1$ values taking these various propensities into consideration. (Mills & Beatty [1979], p. 11)

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After considering some alternatives (for example: the number of offspring which an organism has the *highest* propensity to leave) they end up with the following definition:

> We propose, then, that ''individual fitness'' or ''fitness$_1$'' be defined as follows:

> [(F1)] The fitness$_1$ of an organism *x* in environment *E* equals $n =_{df} n$ is the expected number of descendants which *x* will leave in *E*. (Mills & Beatty [1979], p. 12)

Notice that (F1) is an operationalized version of (C-PIF), for (F1) tries to ascribe a fitness value to an organism. M&B understood that the (general) disposition to reproduce successfully is hardly measurable and applicable for biologists. That is why they developed (F1) as an attempt to operationalize (C-PIF). However, they are not explicit about this fact. I think it is important to explicitly distinguish between a mathematical representation of fitness (as an operationalization attempt) and fitness as a *property* of an organism (dispositional or otherwise), to avoid misunderstanding the notion and also confusions about the nature of the criticisms and objections. For instance, there is a series of counterexamples against the PIF that target (merely) the mathematical representation of the account. Indeed, Pence and Ramsey try to defend the PIF against such counterexamples by developing a new mathematical model for the account leaving what they call *the PIF as a philosophical position* untouched and unchallenged (Pence and Ramsey [2013]).[12] Conversely, my arguments (1-3) against the PIF target solely the account as philosophical position and ignore the mathematical representation altogether.

5 A new proposal

It is important to emphasize that I am not suggesting that there are no dispositions involved in the reproductive success of organisms. What I am saying is that, if one is interested in explanations of the reproductive success of organisms, then dispositions do not provide us with an appropriate way to single out the relevant physical basis and stimulus conditions that cause what I call the *favorable effects*[13] which ultimately result in the reproductive success of the organisms in question. Thus, the question remains somewhat similar to the ones before: What links stimulus conditions to the favorable effects, if the connection between them is not merely statistical (or a matter of frequency)?

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[12] It is important to remark that they are quite aware of and explicit about this distinction and their choice of focusing (merely) on the mathematical model of the account (Pence and Ramsey [2013], p. 856ff).

[13] As the dispositional theories are disputed, I will call these effects 'the favorable effect' (for the lack of better words), because these are the effects that contribute to the reproductive success of the focal organisms.

5.1 A functional approach

Having laid out the problems with the dispositional approach, I want now to turn to an approach which I think can solve the problems. In the last section, I argued that M&B's analogy with solubility does not carry for explanation of the reproductive success of organisms. While we might explain the solubility of salt in water by referring to a certain set of *physical properties* that causes salt to dissolve in water, general explanations of the reproductive success of organisms, I will argue, would consist in reference to *functional properties* of its mechanisms or traits which bring about effects that ultimately result in its survival and successful reproduction. The theory of biological function that I advocate here, the theory of *proper functions,* is Millikan's variation of the so called *selected-effect theory of function* (Millikan [1984]). I will demonstrate that the theory of proper functions has the conceptual tools and theoretical richness to provide us with appropriate answers to the problems above.

However, I should point out that I am not suggesting that *every* explanation of reproductive success or survival involves a reference to functional properties of certain mechanisms. A specific environmental condition could accidently be in favor of an organism, allowing it to improve its chances to survive and reproduce. Or a 'mutated trait' of an organism could produce a specific behavior that is favorable for the individual in its environment and therefore result in its survival. In all the cases of 'accidental effects' as well as effects that count as functions there are some physical or dispositional properties that caused the favorable effect and thus explain the reproductive success of the organism. The point is rather that if the favorable effect is an effect that count as a function, then there is a *principled way* to individuate the set of physical properties that cause the effect in question. This means that these are not just one set of physical properties that happens to produce an effect which is favorable for an organism in specific circumstances and another set for another organism and so on. Rather, there are some *unifying aspects* to one specific set of physical properties that causes the effect in question (let us call it *f*). According to the theory of proper functions, these are properties that *historically caused f* and because of that there is a *positive correlation* between them and *f* which means that there were more organisms in a certain population that had these properties and produced *f* than organisms that did not have them and produce *f*—this is what it means for a trait (with this set of properties) to have been *selected for* doing or producing *f*.[14] For example, according to this

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[14] This is a fairly simplified version of the definition of "direct proper function" developed by Millikan ([1984], p. 28). Because of the highly technical and complex nature of Millikan's definition, I chose this simplified version. It is worth mentioning though that this is not how Millikan come to define and why she defined proper functions. Even so, the important point here is that items that have proper functions "correspond to a pattern that recurs in a large variety of forms, on many levels and in many domains", as Millikan ([2002], p. 115) puts it, which makes certain generalizations about them possible.

theory "birds' wings have the proper function of enabling flight" means, roughly speaking, that wings were selected for flight-enabling effects and "zebras' stripes have the proper function of deterring biting flies" means that they were selected for causing deterrence for biting flies. These are effects that help to explain why birds have wings and why zebras have stripes by explaining how these effects historically contributed to the survival and reproduction of the organisms (of the same lineage) that had them.

Although this theory provides us with a principled way to identify a relevant set of properties that explains the reproductive success of organisms, it is still not clear how it solves the problems that the dispositional theory was facing. Remember that the problem with the dispositional analysis was not that it does not provide us with a mean to individuate a set of properties in a principled way (as we saw, the analysis works fine for solubility of salt in water). The problems were that it does not always identify the *relevant* properties and stimulus conditions for explaining the reproductive success (argument 1, 2 and 3).

5.2 Unraveling the problems with stimulus conditions

To tackle the problems that the dispositional account was facing we should take look out how circumstances of a properly performing proper function and the effect that counts as a function are linked. If the nature of the link is a matter of frequency, as it is in case of dispositions, then we would have the same kind of problems with the functional approach.

As I mentioned before, proper functions of traits are defined through the histories of traits having them. Thus, we should expect that the circumstances of proper functioning of these traits are also determined in specific historical contexts. These circumstances are what Millikan calls *normal conditions*. Millikan defines 'normal conditions' through another technical term, namely *normal explanations*:

> A "normal explanation" explains the performance of a particular function, telling how it was (typically) historically performed on those (perhaps rare) occasions when it was properly performed. Normal explanations do not tell, say, why it has been common for function to be performed; they are not statistical explanations. They cover only past times of actual performance, showing how these performances were entailed by natural law, given certain conditions, coupled with the dispositions and structures of the relevant functional devices. (Millikan [1989a], p. 284f)

Accordingly, a normal condition is defined as follows:

> A "normal condition for performance of a function" is a condition, the presence of which must be mentioned in giving a full normal explanation for performance of that function. (Millikan [1989a], p. 285)

Normal conditions should in no way be understood as average or common. They are not statistically normal. In fact, they are more aptly called *historical success conditions* or, as Millikan puts it, *historically optimal conditions* (Ibid).

Now, let us consider the counter examples against the PIF from the last section. What are the normal conditions under which a vomiting-reflex function is properly performed? These are conditions under which the mechanism of vomiting reflex actually caused organisms to spit out poisonous entities in the past resulting in survival of the individuals possessing these mechanisms. It is obvious that these conditions are not average or common, for otherwise the organisms in question should probably have other ways of constantly dealing with poisons. Yet, this ability would be, in contrast to dispositional theory, included in the set of abilities that contribute to the reproductive success of the organisms that have them, even though it might rarely be exercised. This is because these mechanisms were *selected for* producing the favorable effect and that is the operating principle for this theory and not the appropriate frequency of which the favorable effect is realized.

Furthermore, the theory of proper functions has no problem of differentiating between effects that accidently contribute to reproductive success and those that are functions. Think of the example of the deer hunter from the last section. It would be absurd to assume that deer's hooves have been selected for slipping on ice, causing hunters miss their shots often enough throughout deer's selection history, so that the surviving deer were able to reproduce successfully. And even if this would be the case, then surviving the shot would hardly be an accident, for it would then be the result of natural selection.

In order to eliminate my third objection against the PIF for the functional approach, we shall examine the linkage between normal conditions and effects that count as functions, to see if it supports cases in which traits more often than not fail to perform their proper functions. We already know that normal conditions are linked to proper functions through past cases of the actual success of the traits' ancestors in performing these functions. The question is whether or not the success rate of a function plays a role in determining the normal conditions for performance of the function. And the answer is that it does not. Because, if the trait is selected for, then there ought to be enough successful performances of its function that have contributed to its retention and proliferation (and ultimately to its selection) and the normal conditions are determined through these cases.

The solution to the first argument is somewhat more complicated. As I mentioned in Section 5.1, the functional approach does not account for every case of reproductive success. The cases of 'accidental' success in reproduction and mutated traits that contribute to the reproductive

success but has not yet established through reproduction cannot be explained by the functional approach. That leaves us with the cases of newly learned behaviors. The question is whether or not the functional approach can account for the cases of newly learned behaviors that lead to the reproductive success. The problem with the dispositional theory was that newly learned behaviors produce new dispositions that the theory cannot account for in advance. Does the functional approach have the same problem? The answer is that it does not. However, showing this involves a deeper dive into the theory of proper functions.

The solution has two main parts. First, the mechanisms that produce learning behaviors are selected for producing such behaviors. Second, the function of these mechanisms is above all (at an abstract level) to bring about *relational structures* (i.e. states of affairs that are in specific relations to the focal organisms). Millikan calls this type of proper function "relational proper functions." (Millikan [1984], Chapter 2) For instance, we could say that the function of mechanisms that produce learned behavior through trial-and-error is above all to bring about the same or similar behavior as was rewarded in earlier interactions. Although each of the learned behaviors could differ from the others, they all are results of the proper functioning of (more or less) the same mechanisms producing the same relational structure. The functional approach accounts for the reproductive success achieved through learned behaviors in the same way it accounts for the reproductive success of, say, chameleons achieved through camouflage by changing their skin color to the same color as their immediate surrounding. In other words, in the same way that every new skin color of a chameleon does not have a new function to cause camouflage, every new learned behavior, say, to catch prey does not have a new function of catching prey. Natural selection is less likely to select mechanisms that enable organisms to learn to do only one specific thing, say, *Homo sapiens* to ride a bicycle. Mechanisms that enable humans to learn to ride a bicycle are, probably, selected for various 'balancing advantages' that resulted in better adaption to different environments and better survival; enabling humans to ride a bicycle is not one of their new functions.

However, the same thing could not be said for dispositions. The problem is not that we cannot have 'relational dispositions.' The problem is that every investiture into the relational structure would produce a new disposition with potentially drastically different stimulus conditions. Take, for example, the ability of an organism to learn to catch a prey by, say, hiding in a specific background or by climbing short trees both through trial-and-error. The disposition to hide in that background and the disposition to climb short trees have potentially drastically different stimulus conditions involving different kinds of inner mechanisms with different manifestations conditions. It is even conceivable that the ability of an organism to change its

skin color to match the color of environment would involve drastically different inner mechanisms and stimulus conditions when changing its skin color to match two different surface colors. In that case the dispositions of the organism to change its skin color to one color as opposed to the other would be two different dispositions and the dispositional theory has no tool in its toolbox to prevent this implication.

Having shown that the functional approach does not have the same problems as the PIF, let us now focus on how exactly this approach solve the generality problem and explains the reproductive success of organisms through the functional properties of their traits.

6 Dissolving the 'generality problem'

As I sketched in Section 3.1, the PIF tries to explain evolutionary outcomes as well as evolutionary changes over time and a general explanation of this would solve the generality problem. Furthermore, I argued that the PIF fails to deliver such an explanation (Section 4.1). In the last section I showed that the functional approach is not confronted with the same problems. Yet I still need to show explicitly how the functional approach provides us with a general explanation of selection of trait types, that is, of evolutionary outcomes/changes.

What is to be explained seems to be: (1) the *selection of* traits of type *A* over different traits of type *B* in a population and (2) changes in this disparity over time in that population.[15] For my purposes here I am going to ignore (2), because causes that change disparity in selection of certain trait type, if stable, would (most likely) result in selection of another trait type and is, in general, the same kinds of causes that we are trying to find or describe in explaining (1).

I do not want get into extensive discussion about how selection should be defined. For simplicity, when I am talking about selection here I am *not* referring to a process that result in selection of some entities from a certain pool but the outcome of that process.[16] In light of this, there are three main types of causes of selection: *accidental*, *constitutive*, and *functional* causes. Accidental causes are causes that result in selection of trait types that often called 'genetic drift'. With 'constitutive causes' I want to denote those causes that result in reproduction or retention of so-called *spandrels*.[17] The last type of causes, in which I am primarily interested here, is functional causes. These are causes that result in the reproduction of traits of certain type in a

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[15] (1) and (2) here correspond to (1) and (2) from M&B quotation in Section 3.1.

[16] Selection in this sense is to be distinguished from the technical term "natural selection" which refers to, roughly speaking, selection as a result of variation in population and inheritance of traits.

[17] Gould and Lewontin [1979] and Gould and Vrba [1982]. Spandrels thought to be byproducts of adaptions and natural selection. But whether or not they are byproduct plays no roles in the cause of their reproduction and/or retention. And this seems to be a matter of natural necessity. However, I am not going to discuss spandrels any further in this paper, for they have hardly any relevance for my explanatory purposes.

population because of certain properties of these traits and the effects that these properties bring about throughout the reproduction history of these traits. In this sense we have *selection of* these traits *for* having such properties.[18] In other words, these properties explain why there is a selection of the traits by referring to the effect they have produced throughout the reproduction history of the traits (their proper functions).

Two quick remarks before I try to explain the reproductive success through functional causes. First, these three kinds of causes that I introduce here are not ontological categories. These are (merely) epistemic categories individuated through the types of effects that their corresponding causes produce. There may be some ontological grounds (for some of them) for why they produce specific types of effects. However, I am not going to touch upon that in this paper.

Second, it is conceivable and probable that there would be cases where the causes of selection would be some sort of combinations of the three types that I have mentioned. For example, there may be spandrels that gain functions or traits that have been selected for doing one thing lose their function while continuing to be reproduced as 'free riders' or they gain new functions and so on. The key point is that, as long as these cases could be broken down into these three types, they do not raise any true challenge to the explanatory power of the functional approach.

The difference between the functional approach and the dispositional approach is how they individuate the set of relevant properties and stimulus conditions to explain the selection of traits. For the dispositional theory it is through dispositions, which was, as I have shown, doomed to fail to explain the reproductive success of organisms and consequently the selection of traits. The functional approach, however, individuates the relevant properties through the reproduction history and therefore it can account for reproductive success of the organisms that have them and ultimately the selection of the traits. So the explanation of (1) goes as follows:

> (ERS) Explanation of reproductive success of organisms with the trait type *A* over organisms with the trait type *B* in a population *p*:
>
> a) Traits of type *A* have a certain set of properties that have been reproduced throughout the history of its existence in *p*.
>
> b) These properties bring about certain effect *f* for which the following is true:

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[18] The distinction between *selection of* and *selection for* in this sense is pointed out originally by Elliot Sober. He brings out this distinction in particular to point out that the properties with help of which we individuate selected entities are not always the same properties that cause the selection of the same entities (see: Sober [1984], p. 97ff).

    c) because the traits of type *A* have been producing *f,* the organisms with *A* were able to reproduce more successfully than organisms with *B* in *p*.

It is important to remark that (ERS) lays down the general principle. An extended explanation would probably be more complicated, containing more effects and more traits, for traits are seldom selected for producing a single effect and also because traits co-evolve and there is rarely only one trait that cause the disparity in question. Nevertheless, (ERS) explains the selection of *A*s over *B*s in general by referring to what *As* brings about in its reproductive history. (ERS), therefore, solves the generality problem for biological entities that are selected through functional causes.

7 The metaphor of 'fit': Fitness as an ecological descriptor

Finally, let us take a look at the organism-environment relations that have traditionally been described as a relation of fit. As I showed in Section 2, the orthodox notion of fitness does not say anything about this relation. The metaphor of 'fit' here seems to be a way of trying to capture some kind of normativity. In other words, there is a standard for 'fitting', such that if some aspect of the focal organism matches this standard it 'fits' to its environment. The question from Section 2 was, whether or not there is a respect in which this 'fit-in-relation' explains the evolutionary outcomes in a principled way. In Section 5 I proposed an approach that ultimately explains the evolutionary outcomes in question. Now, does this approach have resources to capture this normativity? If so, then we have an interpretation of the metaphor of 'fit' that is explanatorily connected to the notion of fitness as reproductive success.

    The answer has been given: 'normal conditions' provide us with the required normativity. They set a standard from which a deviation is possible. If the organism's environment *corresponds with* the normal condition for proper functioning of its trait with a proper function, then (per definition) that trait would bring about effect in accordance with 'normal explanations' which means that it fulfills its function which means that (if everything stays the same) the focal organism would reproduce more successfully than organisms without the trait in question.

    The standard for 'fitting' according to this interpretation is fixed through the (reproductive) history of the traits and it is highly context dependent. To have an analogy, it is not like (ahistorical) 'objective' variously shaped 'holes' in the nature that can or cannot be 'filled' with variously shaped traits. The standard of 'fitting' for an organism that should do *x* in order to survive/reproduce in a specific situation is rather the normal conditions of its traits that are responsible for producing *x*. If the organism's current environmental conditions correspond to

those normal conditions, then it 'fits' to its current environment. If not, then either those traits are malfunctioning, or there is a 'mismatch' between the current environmental conditions and the normal conditions.

Lastly, I shall emphasize that I am *not* suggesting that this is how the role of the notion of fitness as an ecological descriptor has traditionally been understood. Indeed, I do not think that Darwin's notion of 'fit' or even for that matter the 'fit' of contemporary biologists actually corresponds to my suggestion above. I am also not saying that they should, for I do not aim at covering all the usages of the term and its theoretical and practical roles in various contexts. What I am suggesting is rather that this is how a 'fit-in-relation' could be interpreted, so that it can explain the reproductive success.

8 Conclusion

The traditional two roles of the notion of fitness cannot be captured by the orthodox notion, because the orthodox notion of fitness does not say anything about the organism-environment relations that are essential to the role of the notion as an ecological descriptor. The propensity notion of fitness tries to explain the reproductive success of organisms by relying on the notion of disposition. If successful in doing so, the propensity theory can rely on the stimulus conditions for manifestation of dispositions to account for the organism-environment relations that explain the reproductive success of focal organisms. However, the propensity theory fails to identify the relevant stimulus conditions for manifestation of the disposition to reproduce successfully. The functional approach, on the other hand, can account for the reproductive success of organisms by relying on the notion of biological function. Relying on the notion of normal conditions, it is possible for the functional approach to identify the relevant stimulus conditions that account for the reproductive success of organisms, hence fulfilling the role of the notion of fitness as an ecological descriptor.

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