Trait-centered vs. fitness-centered definitions of natural selection

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Abstract

During the past few decades, fitness-centered and trait-centered definitions of natural selection have coexisted in the philosophical literature. The former render natural selection definitionally dependent on the presence of fitness differences, where "fitness" is understood as a distinct property from actual reproductive success. On the other hand, trait-centered definitions see selection as definitionally dependent on the presence of a causal relation between a trait (not necessarily fitness) and reproductive success. Interestingly, endorsers of these definitions have rarely – and usually only cursorily – critically engaged the views of the other camp. Therefore, a critical comparison of the two kinds of definitions is lacking in the literature. This paper starts filling this void by opening a discussion about which of the two kinds of definition is more appropriate. I first argue that fitness-centered definitions have difficulties in accommodating cases of opposing selection on correlated traits, whereas trait-centered views have no such problems. To do so, I revisit an old argument put forth by Elliott Sober and I show that recent attempts from the fitness-centered camp to reply to Sober's charge are unsuccessful. I then show that fitness-centered views also have problems with a different type of case, namely opposing selection on a single trait; trait-centered views, on the other hand, may accommodate such cases if, as I propose here, we specify that the causal relation that figures prominently in them is understood as a relation of contributing causation. These arguments suggest that trait-centered definitions of selection are preferable to fitness-centered ones.

Keywords: philosophy of biology; natural selection; fitness; opposing selection; correlated traits; sexually antagonistic selection

1. Introduction

During the past couple of decades, some philosophers have adopted versions of what might be called a "trait-centered" definition of natural selection, according to which selection involves a causal relation between differences in a trait and differences in reproductive success. Interestingly, the recent increase in popularity of this definition does not seem to have hindered

the classical definition that has dominated philosophical discussions of evolutionary biology during the past half a century, namely the fitness-centered definition, according to which natural selection essentially requires differences in fitness, where "fitness" is defined as an ability to survive and reproduce (or as an ability to solve design problems set by the environment) and is therefore construed as a distinct property from actual reproductive success. Indeed, new and perhaps more elaborate versions of the fitness-centered definition have been proposed in parallel with the increase in popularity of trait-centered views.

What seems to have prompted this situation is the fact that authors in either the trait-centered or the fitness-centered camps seem to have developed their views without properly engaging the views of the other camp.[1] This situation has some obvious drawbacks. First, if no direct comparisons between the two kinds of definition of natural selection are made, many readers not directly involved with the issue of defining natural selection might be led to believe that there is no substantive difference between the two kinds of definitions and assume that they are merely different-worded versions of each other. Moreover, it seems quite counterintuitive to develop philosophical understandings of the main notions involved in natural selection (e.g. environment, traits, differential reproduction, relationship with drift) based on an assumed definition of natural selection, without first trying to determine whether this definition is accurate or comprehensive enough. I therefore believe that there is a stringent necessity to discuss about which of the two ways of defining natural selection is more appropriate and the main aim of this paper is precisely to start this discussion.

After briefly presenting the two kinds of definition of selection (Section 2), I will revisit an old toy example from Sober (1984) in order to see how the two types of definition deal with cases of opposing selection on correlated traits and, in so doing, I will show that recent attempts from the fitness-centered camp to accommodate such cases do not succeed (Section 3). I then move on to a different kind of case – opposing selection on a single trait – and discuss (Section 4) how the two kinds of definitions fare with respect to it. I show that while fitness-centered definitions fail to capture cases of this sort, trait-centered definitions need to be slightly amended in order to accommodate them. The amendment that I propose consists in the specification that

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[1] Even the rare authors who did engage the views of the other camp (e.g. Pence and Ramsey 2013, 854-855; Otsuka 2016a, 478) have done so only in passing.

the causal relation that is central to trait-centered definitions be construed as *contributing* causation.

2. Trait-centered and fitness-centered definitions of natural selection

Trait-centered definitions of natural selection constitute a "family" of definitions that vary in subtle ways. According to one trait-centered definition version, natural selection occurs when differences in a trait are causally relevant for differences in reproductive success. Here are a couple of examples:

> by contrast with drift, it [natural selection] is occurring because the physical property differences constituting the hereditary variation that is being differentially reproduced are not merely correlated with differences in reproduction – they are causally relevant to them (Hodge 1987, 251);

> natural selection should be characterized as a discriminate sampling process whereby physical differences between organisms are causally relevant to differences in reproductive success (Millstein 2006, 640).

A similar view is adopted by Godfrey-Smith (2007), but he replaces "causal relevance" with "causal responsibility." More specifically, according to Godfrey-Smith, a phenotypic trait is undergoing natural selection if differences in that trait are responsible for at least some of the differences in reproductive levels. Other authors merely speak of a causal relation or link, rather than of causal relevance or responsibility. Here is an example:

> I presuppose what may be called a causal theory of natural selection, according to which selection acts on a trait just in case (*a*) there is some trait variable, one of whose values denotes the trait, such that this trait variable is a cause of survival or reproductive success, and (*b*) the population includes individuals that vary in respect of that trait variable (Glymour 2011, 244).[2]

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[2] Otsuka (2016a, b) adopts a similar view, though with some potentially problematic nuances (McLoone 2018; but see Bourrat's 2019 reply).

As the above quotations show, one may define selection either by specifying the conditions that need to be met if we are to say that selection is indeed acting (this is the case for Hodge and Glymour) or directly as a kind of process occurring in nature (this is Millstein's case). I do not believe this subtle difference is significant for my goals in this paper.

One will also have noted that the above quotations diverge somewhat with respect to the exact description of the relata that are causally linked in trait-centered views. For one thing, the quoted definitions diverge with respect to what differences need to be caused if there is to be selection: for Millstein and Glymour, it is differences in reproductive success that are relevant for selection, while Hodge speaks more loosely about differences in reproduction and Godfrey-Smith (2007) speaks either about differences in reproductive output or differences in reproductive rates. For my part, I will assume throughout this paper that what needs to be caused if there is to be natural selection (in the trait-centered sense) is reproductive success per unit time. In some cases, the natural unit time will be the generation, but this will certainly not be so for other cases (e.g. for cases where the focal biological individuals differ in generation time).

Similarly, if we claim that selection involves the causing of differential reproductive success per unit time by differences in a trait, one could ask whether all kinds of properties of biological individuals are admissible. Among the above-quoted positions, Hodge and Millstein claim that it is differences in "physical" properties that are relevant for selection, Godfrey-Smith speaks more ambiguously of phenotypic differences, while for Glymour it is the unqualified "traits" that are relevant. This is far from being an insignificant point: indeed, in the absence of a principled way of identifying what kinds of properties are relevant for natural selection, it might prove very hard to even distinguish between natural selection and random genetic drift; and, of course, a definition of selection that fails to distinguish it from drift can hardly be considered a satisfactory definition. But proposals have been made elsewhere about what kinds of property should be seen as relevant for selection (e.g. Godfrey-Smith 2009; Bourrat 2015, 2017; and, more recently, Jeler 2024) and it is not my goal here to go over these proposals or to assess their plausibility. For the purposes of this paper, I will simply assume, following Jeler (2024), that the traits that may legitimately be said to undergo natural selection (in the trait-centered sense) are intrinsic properties of biological entities or extrinsic properties whose possession is causally determined by intrinsic properties or, finally, extrinsic properties that supervene on relations between the intrinsic properties of the members of a biological population. As Jeler (2024) has

argued, this way of circumscribing the traits that are relevant for selection does provide the basis for a principled distinction between natural selection and drift, without thereby ruling out cases that biologists unhesitatingly consider to be cases of natural selection.

While there are certain subtle differences between the trait-centered definitions of selection adopted in the philosophical literature, fitness-centered definitions of selection exhibit an even greater variation. These render selection definitionally dependent on "fitness," where fitness is seen as a property that is distinct from *actual* reproductive success. This is usually done by conceiving fitness as an ability, for example as the ability to solve design problems set by the environment (Bouchard and Rosenberg 2004) or, more popularly, as an ability to survive and reproduce in a given environment, where this ability is conceived as a probabilistic disposition or propensity to leave particular numbers of offspring, with each potential outcome (i.e. offspring number) having a particular probability attached (Brandon 1978; Mills and Beatty 1979).[3] Differences in these abilities are seen by these authors as having causal efficacy, i.e. as being able to cause differences in actual reproductive success.

Authors defending such notions of fitness also defend definitions of selection in which fitness differences play the central role. There are a number of ways in which this has been done. Mills and Beatty (1979) and Brandon (1990) have defended the view that natural selection involves differences in reproductive success that are caused by differences in the ability to survive and reproduce, i.e. by differences in fitness or, as Brandon calls it, adaptedness.[4] Sometimes (e.g. Brandon 2005; and, perhaps less clearly, Mills and Beatty 1979) this first definition is supplemented by adding an "ordinal restriction" to it, i.e. by adding that we are dealing with selection when differences in fitness cause differences in actual reproductive values *and* the ordinal ranking of the individuals or types according to their actual reproductive value

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[3] Other ways of conceiving fitness as distinct from actual reproductive output have been proposed (e.g. Abrams 2012; Triviño and Nuño de la Rosa 2016; Triviño 2024). I will not insist on them here, but what I say about the fitness-centered definitions below applies, I believe, even if the notion of fitness we plug into them is construed along the lines of these other proposals.

[4] Here are a couple of examples: "Selection, properly speaking, involves not just the differential contribution of descendants, but a differential contribution caused by differential propensities to contribute" (Mills and Beatty 1979, 283); "Natural selection is not just differential reproduction, but rather it is the differential reproduction that is *due* to differential adaptedness, that is, due to the adaptive superiority of those who leave more offspring" (Brandon 1990, 11-12). In the non-propensionist camp, Bouchard and Rosenberg (2004) define selection as differences in actual reproductive levels of types caused by differences in their ecological fitness, where, as already pointed out, "ecological fitness" refers to the ability of organisms to solve the design problems set by their environment.

corresponds to their fitness ordinal ranking.[5] Sometimes (e.g. Ramsey 2013, 2015) the mere existence of differences in fitness is equated with natural selection, without any other reference to the actual reproductive success of individuals.[6] Finally, other authors take selection to involve an evolutionary change that is causally determined by differences in fitness (e.g. Abrams 2012).[7]

The consequences of the differences between these versions of the fitness-centered definition would deserve to be studied for their own sake, but this is not something I will pursue here.[8] Here I only want to stress that the main divergence between trait-centered definitions and fitness-centered ones stems from a particularity that "fitness" has when it is understood as distinct from actual reproductive success. Indeed, there is a significant difference between fitness and other traits or abilities: all the causal powers of the other traits/abilities on actual reproductive success are delegated to or reflected in this global "ability to survive and reproduce" called fitness.[9] Fitness is thus a "net" property or phenotypic trait, in the sense that it sums up, into a single quantity, all the causal powers of the other traits on the reproductive output of individuals or types. If one defines selection in a fitness-centered way, one assumes that selection requires differences in this global ability to survive and reproduce (or global ability to

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[5] "Selection is differential reproduction that is due to (and in accord with) expected differences in reproductive success" (Brandon 2005, 169). "Natural selection is occurring in population P in environment E with regard to organisms x, y, z (members of P) $=_{df}$ x, y, z differ in their descendant contribution dispositions in E, and these differences are manifested in E in P" (Mills and Beatty 1979, 283).

[6] Assuming that each individual of a population has a set of possible lives L_i, where each possible life has a particular outcome in terms of offspring production and has a particular probability of occurring, Ramsey (2013, 3914) defines selection as follows: "selection is the inter-organismic heterogeneity in the L_i and is quantified via a function on this heterogeneity." The mere presence of this quantifiable heterogeneity in the possible lives of the individuals of a population is enough to state that selection is at work. Thus, fitness differences are equated with selection: "If there are fitness differences among individuals (and therefore selection)…" (Ramsey 2015, 11).

[7] Abrams (2012, 11) argued that "it is parametric type fitness differences which provide the causal aspect of the process of natural selection in real populations," which means that, for him, natural selection is the causal process by which differences in a particular type of fitness ("parametric type fitness") lead to evolutionary change (i.e. to change in allele/type frequencies or in the average trait value in a population).

[8] Note that authors defending the "statisticalist" view of natural selection (Matthen and Ariew 2002; Walsh, Lewens and Ariew 2002) also embrace a version of the fitness-centered definition. They state: "The process of selection that Darwin postulated is in essence the change in *lineage structure* that occurs when there is variation in *vernacular fitness*. Accordingly, we shall call this phenomenon 'Darwinian selection' (or 'D-selection'). The other process, in which populations change in their *trait distribution* as a function of variation in their *trait fitnesses*, we'll call 'Modern Synthesis selection' (or 'MS-selection')" (Walsh, Ariew and Matthen 2017). While these authors have no quarrel with D-selection, they claim that MS-selection does not involve a causal, but a statistical relationship between fitness differences and trait-distribution changes. They also claim that modern evolutionary explanations are MS-selection explanations and are nor reducible to D-selection explanations. Whether their claims are plausible is not something I can assess here.

[9] "Thus, melanism is one of many physical properties which constitute the fitness, or reproductive propensity, of pepper moths in polluted areas" (Mills and Beatty 1979, 271).

solve environment-set problems) between the individuals or types involved. On the other hand, for trait-centered definitions, selection only requires that there be differences in reproductive success caused by differences in *a* trait, where this latter trait may be any trait,[10] and not necessarily the global "fitness" trait that sums up all the causal powers of the other traits on reproductive success.

It is this difference between trait-centered and fitness-centered definitions that will serve as a guide for my attempt to test how these kinds of definitions fare with respect to opposing selection on correlated traits and to opposing selection on a single trait. To this I now turn.

3. Opposing selection on correlated traits: a problem for fitness-centered definitions

In itself, the net character of fitness I have just discussed is not a problem, given that many other abilities may be said to supervene on other traits/abilities. For example, the ability to run fast supervenes on other properties (including e.g. lung capacity, limb length, tendon and ligament elasticity, muscle strength) and there is no problem in summing all these properties up into a single property. A global property like "fitness" that totalizes the net effects of all the other traits/abilities on reproductive success is therefore not problematic in itself. However, if we define natural selection as a function of differences in fitness between individuals or types, this net character of fitness does open the door to a problem.

A classic example from Elliott Sober (1984, 97) helps circumscribe the problem. Imagine a biological population that is composed of two types of individuals. Individuals of type A are more vulnerable to disease than individuals of type B, while B-individuals are more vulnerable to predation than A-individuals (Sober even supposes that all individuals of a type are clones of one individual). Suppose that the amount of predation and incidence of disease are such that the overall chances of survival are equal for the two types and, assuming that the types do not differ in other evolutionarily significant ways (i.e. in mating success, fecundity etc.), types A and B will thus have the exact same overall fitness. Sober continues:

> Does it follow that no selection process can occur here, since the requisite variation in
> fitness is absent? In a sense that I will try to clarify, the answer is *no*. When we look at

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[10] That is, any trait that belongs to the class of traits that may legitimately be considered relevant for selection (see my brief indications on this point above and, for a detailed discussion, Jeler 2024).

the population, it wouldn't be surprising to learn that the percentage of *A*'s that die of disease exceeds the percentage of *B*'s that die from this cause. Nor would it be a shock to learn that the percentage of *B*'s that fall to predators exceeds the percentage of *A*'s that get eaten. Disease selects against type *A* and favors type *B*, while predation selects against *B* and favors *A*. It's true that there is no *overall* selective difference between the two types, because there is no overall difference in fitness. Nevertheless, there is a good deal of selecting going on. (Sober 1984, 97)

Sober's is an extreme example of opposing selection on correlated traits. It is extreme because it assumes not only that the fitness benefit that a trait provides to a type is exactly offset by the fitness cost of another trait correlated with the first one, but also assumes that this precise offsetting occurs for each and every individual of the population so that all individuals have the exact same fitness. Of course, as Sober (2020) has argued himself, exact values for individual fitnesses are difficult to epistemically access, if not outright impossible. But assuming that we *do* know the fitnesses of two individuals A and B in a given environment, and assuming that we clone them, as Sober stipulates, we could in principle create a case like Sober's and, with all its extreme nature, a definition of selection should be able to accommodate such a case. However, fitness-centered definitions of selection obviously have a hard time achieving this: rather counterintuitively, a defender of a fitness-centered definition of selection has to conclude that there is no natural selection in Sober's toy case, because there are no differences in fitness between the individuals (and types) of the population. No fitness differences, no natural selection.

To my knowledge, no satisfactory reply to Sober's objection has been offered by defenders of fitness-centered definitions of selection. In fact, so far as I know, there are arguably just two attempts to reply to Sober's charge. Both of them are somewhat indirect and, because they are not explicitly aimed at replying to Sober's objection, both are open to interpretation. In order to better grasp the first of these replies – due to Ramsey (2015) – note that one of the aims of Sober's extreme example was that of introducing the important distinction between "selection for" and "selection of" (Sober 1984, 97-102; see also Sober 2013, 2024). Selection-of pertains to the effects of a selection process on the frequency of particular classes of biological entities: to say that a particular sort of object was selected (or that there was selection of a particular type of

individuals) is simply "to say that the result of the selection process was to increase the representation of that kind of object" (Sober 1984, 100). But this does not mean that all the properties that these selected individuals have in common were actually responsible for this increase in frequency or were the targets of the selection process. Another concept is meant to single out the cause of the selection process, i.e. to single out the property that was causally responsible for the increase in frequency of the relevant type of individuals: this is the concept of "selection for." For Sober, a trait is selected-for if possessing that trait increases an individual's survival and reproductive success with respect to individuals that do not possess that property or that exhibit different states for that character.[11] Therefore, it is "selection for" properties that constitutes the proper causal aspect of natural selection (Sober 1984, 100).[12]

This entails that there can be selection for properties without there being selection of particular types of biological entities if the effects of multiple selection-for processes cancel each other out: this is precisely what happens in Sober's example quoted above. But this also entails that, if defenders of fitness-centered definitions were to reconcile their position with the idea of selection for properties, then fitness-centered definitions would be on safer grounds. Ramsey's (2015, 11) attempt at such a reconciliation consists in arguing that "among the traits responsible for the fitness differences, the ones that make a positive difference for fitness are the ones that are selected-for."

However, there are two ways in which this position could be interpreted. According to the first interpretation, Ramsey's position consists in maintaining that when there are no differences in net fitness between individuals or types of individuals, there are no traits

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[11] A selected-for trait is, therefore, for Sober, one that "causes success in survival and reproduction" (1984, 100) or that "is a positive causal factor in the survival and reproduction of organisms" (1984, 280) or that "causally influences reproductive success" (Sober 2013, 339) or, finally, that *makes a causal difference* in survival and reproductive success" (ibid.). This places Sober (1984) in the trait-centered camp when it comes to defining selection.

[12] Let me add that, more recently, Sober (2013, 2020, 2024) has argued that variation in fitness may cause evolution, i.e. it may cause trait frequency change in a population. While this sounds plausible for many cases (though perhaps with some exceptions: see Otsuka 2016b, 262-263), note that, as Sober's (1984) toy example quoted above shows, the absence of fitness variation does not necessarily entail the absence of selection; alternatively, Sober's example shows that the absence of selection of a type (the fact that a type does not increase in representation in the population) does not entail the absence of a selection process. This indicates that neither fitness variation, nor the notion of "selection of" provide the basis for a satisfactory definition of natural selection. But this does not mean that the selection-of concept and the fitness concept are useless for evolutionary theory. Far from it. Indeed, if we want to model the future state of a biological system based on its present state, we need to know what type or types of biological individuals are selected at present (i.e. for what types of individuals there is selection-of at present) and the rate at which they are selected (I will get back to this in my concluding remarks).

responsible for such differences and therefore there is no selection for properties. It is obvious, though, that in this way Sober's problem is not solved, but merely stipulated away. Rather than dispelling our intuition that selection is at work in Sober's example despite there being no fitness differences, according to this first interpretation, Ramsey's point merely stipulates that if there are no fitness differences, then there are no selected-for properties.

But there is a second potential interpretation of Ramsey's point. In Sober's toy case, there are no net fitness differences between the A- and B-individuals, but this null difference in fitness is undergirded by the two resistance traits. Had the B-individuals not exhibited resistance to disease, the A-individuals would have been fitter than the B-individuals; and, conversely, had the A-individuals not been resistant to predation, there would have been fitness differences in the case, favoring the B-individuals. Both resistance to disease and resistance to predation are thus, with Ramsey's term, "responsible" for the null differences in fitness, so, arguably, both are selected-for traits, as Sober claims. But embracing this interpretation would be tantamount to admitting that differences in net fitness are not necessary for there to be selection for properties – and consequently for there to be natural selection in the case at hand; this, in turn, would be tantamount to admitting that fitness-centered definitions of selection are unsatisfactory.

In short, Ramsey's attempt at reconciling fitness-centered definitions with Sober's idea of selection for properties fails, because it consists either in stipulating that there is selection for properties only in cases that can be accommodated by fitness-centered definitions or, according to a second interpretation, in admitting that fitness-centered definitions are wanting.

A second potential attempt to reply to Sober's charge is provided by Abrams (2014). It is even less developed than Ramsey's point discussed above, and it actually only consists in the stating of the definition of selection that Abrams adopts in that article. The definition is the following:

> Natural selection occurs when the frequencies of heritable types (alleles, genotypes, phenotypes) in a population change over time *because* these types have different fitnesses, or when frequencies remain the same *because* the types' fitnesses are the same (Abrams 2014, 133).

The adoption of this definition could easily be interpreted as an attempt to accommodate cases like Sober's. Indeed, in Sober's toy case, assuming that all else is equal (i.e. heritability of relevant traits, mutation and migration rates etc.), one could make a case that, if the frequencies of types A and B remain the same, it is *because* the fitnesses of the two types are the same. Adopting Abrams' (2014) definition could thus provide a way of accommodating Sober's toy case in a fitness-centered definition of selection. However, this comes at a very steep price. Indeed, adopting this definition of selection would entail that there is natural selection in all cases where individuals or types of individuals vary in traits that are *neutral* with respect to reproductive success. To put it otherwise, variation in a trait that is not subjected to any selective pressure will have to be thought of as an instance of natural selection because, in all such cases, assuming all else is equal, if the frequencies of types remain the same, it is because fitnesses are the same. All neutral traits would thus have to be construed as undergoing selection. I doubt that such an unnecessary and potentially confusing expansion of the extension of the natural selection concept would be appealing to most biologists and philosophers.

To sum up, despite recent attempts at defusing it, Sober's charge still poses a significant problem for fitness-centered definitions.[13] On the other hand, trait-centered definitions of selection have no problem accommodating Sober's toy case. Even though there are no *net* differences in survival levels (and, all else being equal, in reproductive success) between A- and B-individuals, differences in resistance to predation and, respectively, to disease *are* causes of differences in reproductive success. Indeed, type A has the same reproductive success as B precisely *because* it is better able to resist predation, otherwise its lower ability to resist disease would have made the A type less reproductively successful than the B type. And the same is the case for the B type: its superior ability to fight disease helps it cancel out the effects on reproductive success of the superior ability of A to resists predators. To put this in interventionist terms, if we increase the difference between the abilities of types to resist predation while holding all other variables fixed, a change in the difference in reproductive success between types will ensue. And the same will occur if we intervene on the difference between the types' resistance to disease (while, again, holding other variables fixed). Selection, in the trait-centered

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[13] Strangely enough, Sober's challenge is sometimes interpreted as stating the exact opposite of what it actually says. For example, McLoone (2018, 11) claims that Sober (1984) defends the idea that "fitness variation is both necessary and sufficient for natural selection to occur." This is a strange claim, given that, as discussed above, Sober's (1984) toy case actually shows that fitness differences are not necessary for natural selection.

sense, thus favors increased resistance to predation and increased resistance to disease, but, because the two traits are negatively correlated, there are no overall net differences in reproductive success and, consequently, no changes in type frequency due to natural selection.

I believe the way trait-centered definitions of selection handle Sober's toy case is highly compatible with scientific practice. Indeed, biologists appeal to natural selection not only for explaining evolutionary change, but sometimes also for explaining the lack of change in trait frequency or variance. As Merilä et al. (2001) note, opposing selection on correlated traits – of which Sober's toy case is an extreme example – is considered to be one of the explanations for evolutionary stasis.

Furthermore, quantitative geneticists routinely see selection as acting on multiple traits at the same time (multivariate selection), and the total effect of selection on the distribution of a trait is given by the effects of direct selection on that trait and the indirect effects brought about by selection acting on other traits that are correlated with the focal one (Lande and Arnold 1983; Arnold 2023; Svensson 2023). This may well lead to cases in which individuals with very different character states for a character z may have the exact same survival rate (i.e. a null selection differential), but this equal survival rate is merely the result of selection acting in opposite directions on correlated traits (i.e. the result of non-zero selection gradients for these traits[14] and of their degree of correlation).

An empirical example of opposite selection on correlated traits – one quite similar to Sober's case – can be drawn from a laboratory study of selection in the water boatman *Sigara falleni* conducted by Candolin (2004). Males of this insect species try to disrupt the attempts to mount females of other males, and this direct competition between males affects their mating success. Males possess a wide-shaped, clawlike tarsal segment on their front legs that is called a foreleg pala. In one of the selective regimes of the study, Candolin (2004) assessed the selective relevance of male body size and male foreleg palae size in male competition. Her results showed that, under male competition, selection favored body size and disfavored pala size: bigger males had a superior mating success, while large pala size decreased male mating success (with selection gradients of similar magnitude and opposite signs for body length and pala size).

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[14] Selection gradients are partial regression coefficients that estimate the effect of a trait on relative survival rate or reproductive success while controlling for other traits. Selection differentials, on the other hand, are simple regression coefficients.

However, as indicated by the selection differential, "no net selection on pala size occurred under male competition" (Candolin 2004, 1862). There were no significant differences in net mating success between individuals with very different pala sizes (or, in any case, no differences that chance alone could not have accounted for); but this does not mean that selection was not acting. Indeed, large palae constituted a disadvantage in male competition. However, because large body size constituted an advantage and because larger individuals also tended to have larger palae, the outcome was that there was no net difference in mating success in the population between individuals displaying palae of different sizes. Like in Sober's toy example above, the direct (negative) and indirect (positive) selection on pala size cancel each other out. Close observations in nature or in the laboratory (or perturbation studies) thus show that selection may be at work even for traits whose variance leads to no *net* difference in reproductive success.

If, in Candolin's case, we were to take two individuals differing in palae size, we might notice that they have the same fitness (and reproductive success). The same would occur if we took two *classes* or *types* of individuals, where the types would differ, again, in palae size. This is why, as was the case with Sober's example, irrespective of whether one defines natural selection as a function of individual fitness (e.g. Ramsey 2013, 2015) or as a function of type fitness (e.g. Abrams 2012), one will be unable to accommodate Candolin's case of opposing selection on correlated traits.[15] There are, however, other examples of opposing selection on correlated traits that only pose a problem for accounts that define selection on the basis of differences in type fitness. In my view, to this category belong cases of sexually antagonistic selection.[16] To take just one example here, let us look at Harano et al.'s (2010) experimental study on the flour beetle *Gnatocerus cornutus*. Males (but not females) of this species develop enlarged mandibles that allow them to be better at fighting other males (Okada and Miyatake 2009) and thus increase their mating success. On the other hand, the genetic architecture of these traits ensures that enlarged mandibles are correlated with reduced abdomen size in males; however, unlike enlarged mandibles, the smaller abdomen size is not a sex-limited trait, and therefore females genetically related to males with large mandibles also develop small abdomens. Harano et al. (2010) showed that females with smaller abdomens have lower lifetime reproductive success, given that abdomen size determines the number of eggs that a female can carry. We are thus dealing with a

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[15] The same holds for the cases of opposing selection on a single trait that I will analyze in the next section.
[16] An anonymous reviewer helped me clarify this point.

case of sexually antagonistic selection: females with small abdomens are directly selected against (via decreased fertility), while males with small abdomens are selectively favored because of direct selection for enlarged mandibles (via increased mating success), which are correlated with smaller abdomens. Under the right conditions, we may thus very well see the effects of sexually antagonistic selection balance each other out (Lande 1980; Bonduriansky and Chenoweth 2009), and we may thus have a situation in which the positive benefit of enlarged mandibles in males is exactly offset by the cost of the correlated small abdomens in females. In this case, there is a difference in reproductive success (and fitness) between individual organisms (two males with different abdomen sizes differ in fitness and reproductive success; similarly, two females with different abdomen sizes will differ in fitness and reproductive success). However, there is no net difference in reproductive success (and fitness) between the *types* of the population: the class of individuals possessing reduced abdomens will, on average, have the same reproductive success (and fitness) as the class of individuals possessing larger abdomens. The absence of a net difference in reproductive success (and fitness) between types is a symptom of (sexually antagonistic) selection, rather than an indicator of the absence of selection.[17] But here as well, differences in mandible size and differences in abdomen size are causes of differences in reproductive success, and a trait-centered definition of selection thus has no difficulties in accommodating this kind of case.

Cases of opposing selection on correlated traits therefore pose no problem for trait-centered definitions of selection, while they pose a significant difficulty for fitness-centered definitions.

4. Opposing selection on the same trait: amending trait-centered definitions

We now need to determine whether fitness-centered and trait-centered definitions manage to accommodate cases of opposing selection on a single trait. It would be a serious problem if they could not accommodate such cases, given that biologists certainly do not hesitate to speak of opposing selection in cases in which a particular trait increases and decreases – on two different pathways – the reproductive success of its bearers. Life history theory in particular abounds in examples of this sort. Schluter, Price and Rowe (1991), for example, provide a list of

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[17] This is one of the reasons why theorists of intralocus sexual conflict speak of its "cryptic nature" (Bonduriansky and Chenoweth 2009, 280).

field studies in which a single trait enhances one component of the reproductive success of the focal individuals, while also reducing another component; for them, these studies document cases of opposing selection, even though the same trait is selected for and selected against by different pathways.[18]

The above discussed study of sexual selection in the water boatman, *Sigara falleni* (Candolin 2004) provides a striking example of opposing selection on a trait. Males of this species court females by shaking their bodies and their foreleg palae in front of females. Along with the male competition selection regime discussed above, Candolin (2004) also imposed another selective regime in the laboratory, one aimed at determining the effects of body size and forleg palae size on female choice (and, consequently, on male mating success). According to her results, female choice favored large body size and large foreleg palae (positive selection differentials for both of these); but in this selective regime there was only selection for larger foreleg palae, whereas body size was only selected because males with larger palae tended to also have a larger body size (otherwise put, only the selective gradient for pala size was significant). Female choice thus directly favored large palae size and indirectly favored large body size, whereas Candolin's other selective regime discussed in the previous section – that of male competition – directly favored both small palae size and large body size. Therefore, the exact same trait – foreleg pala size – is directly selected for by female choice and directly selected against by male competition. So, under female choice and male competition, a single trait may be subjected to opposing selection. Candolin (2004, 1864) concludes that "the opposing selection on the sexually dimorphic trait, foreleg pala size, could contribute to the maintenance of genetic variation in the trait by resulting in (…) no net selection."[19] To put it otherwise, it may happen – if the conditions are right – that the mating success benefit brought about by large foreleg palae via female choice be exactly cancelled out by the mating success cost brought about by large foreleg palae via male competition.[20] But the fact that the positive and negative

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[18] Also, many cases of sexually antagonistic selection are cases in which the exact same trait or allele(s) are selectively favored for one sex and disfavored for the other sex (see, e.g., Connallon and Clark 2014a, b; Cox and Carlsbeek 2009; Merilä et al. 1997).

[19] Or, she adds, it could lead to "disruptive selection on the trait, especially if the strength of selection varies in time or space" (Candolin 2004, 1864).

[20] Exactly how often the "right" conditions may occur in populations in the wild is difficult to say. When it comes to sexually antagonistic selection, some biologists believe that they may be frequent. For example, Connallon and Clark (2014a, 5) state: "Estimates of selection on single traits suggest that opposing directional selection is common, and often of similar magnitude between the sexes."

effects of a trait on reproductive success cancel each other out does not prevent such cases from being ones of opposing selection.

Now, note that if Candolin, as well as life-history researchers such as those listed in Schluter, Price and Rowe's (1991) survey of cases of opposing selection on a trait are right to claim that there is selection going on in such cases, then putative definitions of selection must be able to accommodate such cases. It is easy to see that fitness-centered definitions have troubles accommodating them. To better see this, suppose we have a population of *S. falleni* in which males either have large foreleg palae (let us call these type X) or small foreleg palae (type Y). Opposing selective pressures from female choice and male competition ensure that types X and Y have the same mating success and, all else being equal, the same fitness. No differences in fitness means no selection, according to fitness-centered definitions. So, faced with cases of opposing selection on a trait, a defender of a fitness-centered definition would have to propose a solution for accommodating such cases or would have to claim that biologists like those gestured towards above are in error when speaking of selection in such cases. To my knowledge, neither of these two potential defenses of fitness-centered definitions has been put forth in the literature.

It is interesting, however, to note that cases of opposing selection on a single trait potentially raise a problem for trait-centered definitions too. Again, take the same case in which opposing selective pressures from female choice and male competition ensure that the mating success and, all else being equal, the reproductive success is the same for types X (large foreleg palae) and Y (small palae). The problem is that, in this kind of case, we cannot simply say, as we did in cases with opposing selection on correlated traits, that intervening on the difference in foreleg palae size between the two types would alter the difference in reproductive success between the types: indeed, such an intervention leads to no *net* difference in reproductive success between types in our case. Cases with opposing selection on one trait thus seem to pose a similar problem for trait-centered views to the one posed for fitness-centered definitions by Sober's case of opposing selection on correlated traits. Also, note that appealing to Sober's notion of selection-for does not help us avoid the difficulty. Recall that, for Sober, a trait is selected-for if possessing that trait makes a causal difference to reproductive success with respect to members of the population that do not possess the trait (or have different states for the character). However, in my example of opposing selection on a single trait, possessing large palae does not make an obvious difference to reproductive success, because the individuals of type X (large

palae) and those of type Y (small palae) have the same reproductive success. This marks a significant difference between cases of opposing selection on correlated traits (like Sober's classical example) and the cases of opposing selection on a single trait that I discuss here.

What I want to suggest in what follows is that trait-centered definitions may avert the problem if we were to add a specification to the causal relation such definitions usually contain. Indeed, existing definitions, like the ones I listed at the beginning of this paper, are somewhat vague when it comes to spelling out the causal relation between differences in a trait and differences in reproductive success. Hodge (1987) and Millstein (2006) only require that differences in a trait be "causally relevant" for differences in reproductive success. However, "causal relevance" may have many meanings: McKitrick (2005) inventories no less than nine meanings for causal relevance and most – if not all – of these meanings lead, if taken at face value, to the same problem mentioned above, namely that the difference in foreleg palae between the members of our population of *S. falleni* turns out not to be causally relevant for their differences in reproductive success. A similar vagueness is characteristic of Godfrey-Smith's "causal responsibility" notion. However, Glymour's minimal conditions for saying that selection is at work – namely that there be variation in a trait which is "a cause" of variation in reproductive success – might be more readily available to specification in order to not rule out cases like the one discussed here.

Indeed, in the interventionist framework of causation adopted by Glymour (as well as Otsuka), more specific notions of "cause" are available. For my purposes here, it is enough to follow Woodward (2003) in distinguishing between a total cause, a direct cause and a contributing cause. A cause C of effect E is a *total* cause if an intervention on C will change E (or the probability distribution of E). The difference in foreleg palae in the case under consideration here is not a total cause, because increasing or decreasing it will, by hypothesis, not alter the difference in reproductive success between the males of the two types. Whether a cause is a direct cause or not depends on the set of variables one chooses to model. A *direct* cause C of effect E is one whose modification changes the value or the probability distribution of E, when all the other variables in our set are held fixed at some value. Is the difference in foreleg palae in our case a direct cause of the difference in reproductive success? No, it is not, because, following Candolin, it is already specified that there are other variables (namely, the ability to attract

females and the ability to fend off other males) that are determined by foreleg palae size[21] and that serve as intermediaries between differences in foreleg palae size and differences in reproductive success. (One could object that the "abilities" to attract females and to fend off competing males are properties that are not caused by foreleg palae size, but *supervene* on foreleg palae size. I disagree. While I call these "abilities" for ease of communication, they can be conceived – and are actually conceived by Candolin – as quantitative variables like "number of females convinced to stop resisting copulation" or "number of males whose mounting attempts have been disrupted or whose attempts at disruption have been neutralized." Such variables do not supervene on, but are effects of foreleg palae size.)

The difference in foreleg palae size is neither a total, nor a direct cause; rather, it is a contributing cause of differences in reproductive success. According to Woodward, cause C of effect E is a *contributing* cause if there is a directed path between C and E – such that each link in the path is a direct causal relationship – and if intervening on C while holding fixed all the other variables in the set that are not on this path will lead to a change in E. Woodward's notion of contributing cause is meant to do justice to the intuition that a variable may be a cause of an outcome even if it promotes the outcome on one pathway, while it inhibits it on another pathway so that, on the whole, the two influences of the cause on the outcome cancel each other out. In other words, it is meant to capture the intuition that failures of "faithfulness" (Spirtes et al. 2000) do not rule out causation.

This is precisely the situation of opposing selection on a trait. The large palae size of type X males increases their ability to attract females, even though it decreases their ability to fend off males. But if we were to increase the difference in foreleg palae size between types while holding fixed the difference in their abilities to compete with other males, we would notice a change in the difference in reproductive success between the two types of males, i.e. the reproductive success of males would cease to be equal and males of the X type would have the upper hand. Conversely, males with smaller palae would gain the upper hand if we were to increase the difference in palae size between types while holding fixed the difference in their ability to attract females. The difference in foreleg palae size between males is therefore a contributing cause of differences in reproductive success. So, if biologists are right to consider

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[21] Note that the values taken by these other variables may also depend on other factors, not just on foreleg pala size (for example, as Candolin establishes, the ability to fend off other males also depends on body size).

that such cases are cases of opposing *selection*, then we have to add a specification to our trait-centered definition of selection: what is required for selection is not merely an unspecified causal relationship or the causal relevance/responsibility of a difference in trait for a difference in reproductive success; what is required is that the difference in trait be a contributing cause of the difference in reproductive success. Selection is therefore not the mere causing, but the contributing causing of variance in reproductive success per unit time by the variance in a trait.

To sum up, cases of opposing selection on a single trait pose a significant problem for fitness-centered definitions of selection, but they pose no problem for trait-centered definitions as long as the causal relation that is at their core is specified as a relation of contributing causation.[22]

5. Concluding remarks

Above, I argued that fitness-centered definitions are unsuitable *qua* definitions of natural selection. But my claim only refers to definitions that place at their center a notion of fitness construed as distinct from actual reproductive success. Indeed, when biologists themselves spell out the conditions for (evolution by) natural selection, the notion of "fitness" usually figures prominently among these conditions. For example, one of Lewontin's (1970; 1985) highly influential three conditions for evolution by natural selection is that of "fitness differences" or "differential fitness" between phenotypic variants. Similar conditions are to be found in influential evolutionary biology textbooks (e.g. Futuyma 2005; Ridley 2004). However, in the context of identifying conditions for (evolution by) natural selection, these biologists define fitness as a mathematical function of actual reproductive levels. For example, by "differential fitness," Lewontin (1985) understands the fact that "different variants leave different numbers of offspring either in immediate or remote generations." Similarly, Futuyma (2005, 272) defines

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[22] I do not claim to have discussed here all types of case that are problematic for fitness-centered definitions without being so for trait-centered definitions. An anonymous reviewer wonders whether a case from Otsuka (2016b, 262-263) is also of this sort. In that scenario, a trait *T* does not causally contribute to reproductive success; rather, trait *T*, as well as the reproductive success and fitness value, are affected by a common cause, namely an environmental factor. There will be a systematic difference in reproductive success in this scenario (with the type possessing *T* outreproducing the other), but this will not lead to adaptive evolution. Now, it is obvious that, according to a trait-centered definition, this is not a case of natural selection, since trait *T* is, by hypothesis, not a cause of reproductive success. But would a fitness-centered definition categorize this as a case of natural selection, given that the type possessing *T* has a higher fitness than the one without the trait? It might, but this is contingent upon one's view on what the relevant environment for natural selection is, and there is also some variation on this issue in the fitness-centered camp. I cannot delve deeper into this problem here.

genotypic fitness as "the average lifetime contribution of individuals of that genotype to the population after one or more generations," whereas Ridley (2004, 74) defines (relative) fitness as "the average number of offspring produced by an individual relative to the number of offspring left by an average member of the population." Therefore, the use of the term fitness in these influential accounts of the conditions for (evolution by) natural selection may not be seen as an argument in favor of fitness-centered definitions. On the contrary, the meaning attributed to the notion of fitness in these accounts renders them much closer to trait-centered than to fitness-centered definitions.

It is also important to clearly stress what I did *not* contest here. By claiming that fitness-centered definitions of selection are not suitable ones, I *only* contested the role of fitness – understood as distinct from actual reproductive success – as a definiens of natural selection. I did not, in any way, contest the crucial importance of fitness in evolutionary biology, nor did I contest its adequacy at fulfilling other roles in evolutionary biology. Indeed, fitness is a central concept for determining the evolutionary dynamics of populations (Krimbas 2004). Together with information and/or assumptions about other factors (environmental stability or variation patterns, heritabilities of traits, mutation rate, migration, recombination etc.), fitness differences are crucial for inferring future evolutionary changes or equilibrium frequencies.[23] But which fitness notion is compatible with this role? Is the fitness notion that evolutionary biologists use when predicting evolutionary changes/equilibrium merely a heuristic device, a mathematical expectation regarding the future reproductive success of types in a given populational and environmental context, as Krimbas (2004) argues? Or is it a more substantial property attributable to the individuals or types involved, the kind of inherent "ability to survive and reproduce" that philosophers theorize in various ways? Or, finally, is the "fitness" used by biologists when inferring evolutionary dynamics compatible with both the heuristic and substantial notions of fitness? I would not be surprised if the latter of these positions turned out to be the easiest to defend. But this discussion is beyond the scope of this paper. I did not contest the fact that the notion of fitness understood as different from actual reproductive success may play other important roles in evolutionary theory.

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[23] In Sober's (1984) terms, we could say that knowing that there is "selection of" a particular type of individuals (and the rate at which that type is selected) is crucial for inferring future states of the system in question.

A notion – even one as important as that of "fitness" – cannot be expected to do everything,[24] and I only argued here that this notion is not appropriate for playing a central role in the definition of natural selection. In other words, I argued that trait-centered definitions of selection are preferrable to fitness-centered ones. I showed that, unlike fitness-centered definitions, trait-centered ones have no problem accommodating cases of opposing selection on correlated traits. Moreover, I showed that, unlike fitness-centered definitions, trait-centered definitions also accommodate cases of opposing selection on a single trait, provided that the causal relation figuring prominently in trait-centered definitions is understood as a relation of contributing causation. These arguments lend support to the idea that trait-centered definitions of selection are preferable to fitness-centered ones.

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[24] See Otsuka (2016a; 2019) for arguments pointing in the same direction.

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