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Philosophy of Science, Vol. 61, No. 3 (Sep., 1994), 475-486.

DISCUSSION:

SOBER ON BRANDON ON SCREENING-OFF AND THE LEVELS OF SELECTION*

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Sober (1992) has recently evaluated Brandon's (1982, 1990; see also 1985, 1988) use of Salmon's (1971) concept of screening-off in the philosophy of biology. He critiques three particular issues, each of which will be considered in this discussion.

1. Screening-Off and Explanation. E. Sober (1992) has recently evaluated R. Brandon's (1982, 1990; see also 1985, 1988) use of W. Salmon's (1971) concept of screening-off in the philosophy of biology. Sober is critical of (1) Brandon's claim that factors that screen off others from an event provide better explanations of that event than those that are screened off; (2) Brandon's use of screening-off to explicate the notion that an asymmetry exists between phenotype and genotype with respect to reproductive success in typical cases of organismic selection; and (3) Brandon's use of screening-off to characterize the levels of selection.

Brandon has essentially adopted Salmon's (1971, 1984) views on screening-off and their relevance within the theory of explanation. Thus Sober's discussion of (1) criticizes Brandon's use of Salmon's theory of explanation rather than anything original in Brandon's work. Rather than defend Salmon here, we show that Sober's critique is based on a partic-

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*Received June 1992; revised January 1994.

†The authors are members of the Research Triangle Philosophy of Biology Discussion Group. We wish to thank the National Humanities Center for hosting our discussions during the 1991–1992 academic year.

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Philosophy of Science, 61 (1994) pp. 475–486

ularly unsympathetic reading of Salmon, then we make a point about screening-off, causal interactions and explanation not made by Salmon, but one to which we think he would be sympathetic. (We note that Sober does not refer to Salmon 1984 in which Salmon's views extend well beyond his earlier article. This will be discussed below.)

Sober's examples of screening-off involve chains of discrete events, for example, "My dialing your number causes your phone to ring; your phone's ringing causes you to answer it" (1992, 142). By definition, P screens off D from E iff $\Pr(E, P \& D) = \Pr(E, P) \neq \Pr(E, D)$. In Sober's case the proximal cause P (your phone's ringing) screens off the more distal cause D (my dialing your number) from the effect E (your answering the phone) when and only when this definition is satisfied. Sober correctly points out that in such chains of events proximal causes will not always screen off distal causes. For them to do so "[t]he chain must have solely intermediate probability values and the event in the chain at time t must exhaust the causal facts at time t pertinent to the occurrence of later events in the chain" (ibid.). Technically nothing is wrong with such examples, but one of the major points of Salmon (1984) is to explicitly develop the ontological view that underlies his theory of explanation. That ontology is one of causal processes and causal interactions, not one of chains of discrete events. Salmon approvingly quotes J. Venn as saying, "Substitute for the time honoured 'chain of causation,' so often introduced into discussions upon this subject, the phrase a 'rope of causation,' and see what a very different aspect the question will wear" (quoted in Salmon 1984, 183).

What is this different aspect? Sober naturally (*given* the examples he takes as paradigms) asks whether screening-off factors are always more explanatory than screened-off factors with respect to the event to be explained:

> In causal chains in which any two links are screened-off from each other by any link that occurs in between, the screening-off requirement takes one closer and closer to the effect itself. Between the phone's ringing and your answering it, there was your forming the intention to answer the phone. Are we compelled to say that your having the intention to answer the phone on that particular occasion is a better explanation of why you did so than either the fact that the phone was ringing or that I dialed your number? I see no reason to think this. . . . (1992, 149)

This would pose a serious problem for Salmon's view if we think in terms of chains of events. Indeed this problem was raised (in a slightly different context) by B. Russell. Russell (1918) pointed out that if we think of causation in the following way: *E1* causes *E2* iff whenever *E1* occurs, *E2* follows after a time interval *t*, then we are faced with a problem. The problem is that we can diminish the interval *t* and find a more suitable cause, *E1′*, of *E2*; and, according to Russell, we can continue to do this indefinitely since the time series is compact. Sober raises just this problem: Given events *D*, *P*, and *E*, if the screening-off requirement tells us to explain *E* in terms of *P* instead of *D*, there will always be an event *P′* located between *P* and *E* on that chain such that screening-off requires us to explain *E* in terms of *P′* instead of *P*. Thus, Sober seems to say, screening-off is not an adequate or accurate guide to explanatory power.

If we switch from an ontology of events to one of causal processes and causal interactions, does the same problem arise? For Salmon (1984, 139–157), a causal process persists through space and time; it is capable of transmitting its own structure through space and time. An organism is a pertinent example of a causal process, but a simpler example would be a baseball. A baseball transmits its shape, color, size and momentum, as well as other properties, through space and time. Consider a baseball flying toward home plate. To keep things simple, suppose that the baseball is moving through a vacuum within an inertial reference frame, so Newton's laws describe the motion of this baseball without further complication. In particular, according to Newton's first law, the ball's velocity will remain unchanged unless and until it interacts with something else. For Salmon (ibid., 168–174), a causal interaction is the spacetime intersection of two or more causal processes that modifies the properties of both of those processes. A bat hitting a ball is a paradigm example of a causal interaction. Salmon's basic idea is that if we want to explain the trajectory of the ball after it and the bat meet, we need only cite that causal interaction of ball and bat. States of the ball prior to the interaction are screened off by the interaction, and, given our idealizations in this example, states of the ball after the interaction (excluding its spacetime coordinates) remain unchanged. Thus, if our explanandum is the momentum of the ball two seconds after its interaction with the bat, nothing is gained by diminishing that time interval to get closer to the explanandum and screening-off does not apply to any intermediate time slice of the ball. For example, the state of the ball one second after its interaction with the bat *does not* screen off the interaction from the explanandum. So Russell's and Sober's problem does not arise.

However, one might think the problem, or something like it, does arise in real ballparks where balls have to move through an atmosphere within a gravitational field. There the ball interacts countless times with molecules (and atoms and subatomic particles) as it moves through the air, and so the time interval between the ball-bat interaction and two seconds later can be divided a large number of times based on the large number of causal interactions between the ball and the particles within the atmosphere through which it moves. Are we then driven to explain the momentum of the ball two seconds after it was hit in terms of an interaction between it and a minute particle two seconds minus a nanosecond after the hit? We do not think so. We do not try to explain the momentum of the ball after it is hit in such terms for two reasons. First, it is practically impossible. Second, it is (thankfully) unnecessary. The countless interactions, each having only a minute effect on the ball, can be treated statistically where the relevant macroproperties are wind speed and direction, barometric pressure, temperature and relative humidity. (These are the macroproperties of the medium through which the ball travels; this, of course, takes place within a gravitational field.) Thus we explain the trajectory of the ball after it is hit in terms of that major interaction and the prevailing *conditions* (such as wind and barometric pressure). It might be thought that the line we are taking with respect to this example introduces a pragmatic element into the theory of explanation, in contrast to Salmon's stated aim of an objectivist theory (ibid., chap. 1; 1989). If so, so be it. But we point out that it is an *objective* feature of our world that some interactions have major effects and others have only very small effects that can be treated statistically (and, realistically speaking, *can only*, be treated statistically).

Brandon adopted from Salmon the basic idea that change in the world is produced by causal interactions, that explanation of such change should be framed in terms of the relevant causal interactions, and that screening-off is a useful tool in getting at the relevant interactions. In the biological context, a certain level of fitness or adaptedness results from an interaction between a biological entity and its selective environment (see Brandon 1990, esp. chap. 2). Natural selection results from *differences* in the interactions of different entities within a common selective environment. Screening-off is, according to Brandon, a useful tool in getting at the levels of biological organization at which such interactions occur. We explore these claims in the next two sections.

2. Screening-Off and the Asymmetry between Phenotype and Genotype. Brandon (1982) suggested that screening-off could be used to give a precise explication of the intuition expressed by Mayr (1963), "natural selection favors (or discriminates against) phenotypes, not genes or genotypes" (p. 184). Mayr's view—shared by most, but not all, evolutionary biologists—is that selection acts directly on things such as height, flower number or developmental rates, not genes. Gould (1980) reiterates this point: Genes are not *directly visible* to natural selection, only bodies (or phenotypes) are. But one might object to all this by arguing that genes cause phenotypes which cause a certain level of reproductive success;

therefore, genes are as causally responsible for a certain level of reproductive success as phenotypes (assuming the transitivity of causation), and so they are selected as directly as phenotypes. It is to this argument that Brandon (1982) replies, using screening-off to demonstrate an asymmetry between phenotype and genotype with respect to reproductive success. (We should note that neither Mayr nor Gould consider this argument, and so, of course, do not respond to it.) Screening-off is obviously an asymmetrical relation and so if it can be shown that phenotypes generally do screen off genotypes from reproductive success, then we can justify Mayr's and Gould's claims about selection acting directly on phenotypes instead of genotypes. (If **A** screens off **B** from **E**, then **B** does not screen off **A** from **E**. That is the asymmetry. Once **E** is fixed, then screening-off is an asymmetric two-place relation. Of course, if **E** is allowed to vary, then screening-off is a triadic relation which is asymmetric for two of its three unordered pairs.)

Do organismic phenotypes generally screen off genotypes from organismic reproductive success? Despite some minor points raised by Sober, we argue that they do, that is, that the following relation generally holds among phenotype **p**, genotype **g**, and level of reproductive success **n**:

$$\Pr(\mathbf{n}, \mathbf{p} \,\&\, \mathbf{g}) = \Pr(\mathbf{n}, \mathbf{p}) \neq \Pr(\mathbf{n}, \mathbf{g}).$$

Sober's first worry is that "the description of the phenotypic properties *P* must be *complete*; otherwise, there is nothing to prevent a genotypic specification from affecting the organism's prospects for survival even after the phenotypic character is taken into account" (1992, 143). This caveat is based on a confusion we will see again shortly. Descriptions and specifications do *not* affect organisms' survival and reproduction; they can only affect our understanding of such things. Put another way, the *objective* probability of **n** for *this* organism with *its* phenotype is unaffected by how well or how completely we describe its phenotype, although, of course the *subjective* probability is so affected. Brandon (1978, 1990) explicitly argues that objective probabilities are required in this context; he and others have argued for the *propensity interpretation of fitness* in which the relevant probabilities are objective propensities (see Richardson and Burian 1992). Here Brandon's use of screening-off differs from Salmon's in that Salmon advocates a frequency interpretation of probability. One major difference between the frequency and propensity interpretations of probability, and the difference relevant to the present discussion, is how they deal with the problem of the *single case*. The propensity interpretation claims to make sense of objective single-case probabilities; indeed, such probabilities are analytically basic for that interpretation. For instance, a unique coin tossed only once and then destroyed has a definite probability of heads that is independent of our knowledge of it, and independent of any other tosses of any other coins. In contrast, in the frequency interpretation Salmon favors, what is analytically basic is the limit of the relative frequency of heads in the (hypothetical) infinite sequence of tosses of that coin. Our response to Sober makes the philosophically controversial assumption that objective single-case propensities make sense. Although we will not defend that position here, we note one powerful argument for the propensity interpretation of probability which comes out of recent work in philosophy of biology, namely, that evolutionary theory seems to require it (ibid.; see references therein). This, of course, is analogous to Popper's (1959) original argument for the propensity interpretation; he argued that quantum theory requires it.

Second, Sober writes, "the genotype must not confer a probability of unity on the phenotype" (1992, 143). This is an obvious point; and since there are only rare exceptions to it (e.g., unconditionally lethal genes), we do not see it limiting Brandon's intended application of screening-off. Sober continues:

> [T]his means that we are describing genotypes that have nonflat norms of reaction; varying the environment must have some effect on the resulting phenotype. The probability model implicitly assumes that there is a nonzero probability that the organism live in some environment different from the one it actually occupies and that this change in environment would affect the phenotype. (Ibid.)

Here Sober is simply wrong. Although the model allows that environmental variation can cause phenotypic variation, it need only assume that development is noisy. In this world, that is a safe assumption (see Waddington 1957, Falconer 1981, Lewontin 1983, Mitton and Grant 1984, West-Eberhard 1989, and Smith 1992). Thus Sober's second objection seems to be that phenotype *need not* screen off genotype—that we can imagine possible biologies where it would not. But why this would be seen as an objection escapes us since one of the major themes of Brandon (1982, 1988, 1990) is that selection can occur at a number of levels of biological organization, including levels both below and above that of the individual organism. Thus Brandon is committed to the view that organismic phenotype *does not* always screen off genotype from organismic reproductive success; it does so only in cases of *organismic selection.*

Another point Sober raises is that "Brandon's screening-off requirement attempts to establish by formal means an asymmetry that is not formal, but (if anything) biological" (1992, 150). We agree that the asymmetry is biological and not formal since it is only because of deep and general, but contingent, facts about biology that organismic phenotype screens off genotype from organismic reproductive success (when it does, which is not always). But we fail to see why Sober thinks that the use of screening-off in this context should imply otherwise. On our view the probabilities involved reflect contingent objective facts about the relevant biological system; clearly they are not derived from *formal* features of the system or from the syntax of our language describing the system. Even if one accepts Sober's (implicit) subjectivist reading, the relevant probabilities derive from the subjective probabilities of particular outcomes given our understanding of the causal processes at stake. The fact that we can usefully describe the asymmetry between phenotype and genotype using the formal apparatus of screening-off does not imply that the generalization is anything other than biological. (Does a biological generalization described in mathematical terms suddenly become mathematical, rather than biological?)

Sober's final objection is reminiscent of his first. Sober grants that ("in many cases" [ibid., 149]) phenotype screens off genotype from organismic reproductive success, "but if we shift to a different *explanandum*, the asymmetry may be erased or reversed" (ibid.). For instance, if the explanandum is change in gene frequency, rather than organismic reproductive success, then, since in certain population genetic models genic fitnesses *mathematically determine* change in gene frequency and phenotype does not, genotype would screen off phenotype with respect to that explanandum. In an earlier work Sober (1984, 229–230) has raised this same criticism and Brandon (1990, 85) has responded to it. The essence of that response is that Sober's criticism is based on a simple equivocation between mathematical determination in a model and causal determination in the world. With respect to Brandon's use of screening-off, only the latter is relevant. (The connection between this objection and the first is that in both Sober is concerned with how certain information might affect our epistemic or subjective probabilities whereas according to both Brandon and Salmon, the ontic or objective probabilities matter.)

Thus we conclude that in the real world, though perhaps not in Sober's "real world of evolutionary model building" (1992, 150, fn. 4), phenotype screens off genotype from organismic reproductive success (in those cases correctly classified as organismic selection). As philosophers of biology and practicing evolutionary biologists it is the real world—the world of organisms, and perhaps biological entities at other levels of organization, interacting with their selective environments—in which we are ultimately interested. Models are simply tools we use to get at the real world.

3. Screening-Off and the Levels of Selection.

Sober says:

> Mayr is basically right about the relationship of genotype, phenotype, and an organism's reproductive success, but this is not the basis for

> resolving the controversy over group versus organismic adaptation. Indeed, Mayr does not claim that the causal asymmetries in the chain from genotype to phenotype to reproductive success settle that matter. (1992, 148)

Since Sober attributes Brandon's position to Mayr (incorrectly, see sec. 2, par. 1), and since he agrees with that position vis-à-vis the asymmetry between phenotype and genotype with respect to organismic reproductive success, Sober's main criticism of Brandon's work seems to be that although screening-off does help show how genic selectionism goes wrong, it has little or no relevance for the units or levels of selection question. First we will explain why we think an answer to the genic selectionist question should also serve as an answer to the levels of selection question. Then we will address some of Sober's specific criticisms.

There has been extensive discussion of the sort of genic selectionism advocated by Williams (1966) and Dawkins (1976), which we will not rehearse here. Suffice it to say that at least part of the controversy surrounding this issue concerns the causal process of selection and how it can be adequately explained. The genic selectionist argues that garden-variety cases of selection—what we call organismic selection—can be fully explained in terms of causes acting at the genic level. The "directness" argument against this (defended by Mayr, Gould, and Brandon) says, on the contrary, that selection typically cannot "see" genes or genotypes and acts instead at the phenotypic level. Thus, according to Brandon, an adequate causal explanation of organismic selection must be given in terms of phenotypic differences since they screen off genic or genotypic differences. That is, the causal interactions that underlie selection are at the level of the organismic phenotype. Now when we turn our attention from standard cases of organismic selection to cases of selection acting at other levels of biological organization the basic question remains the same. At what level(s) of organization are the relevant causal interactions taking place? Brandon argued that screening-off is helpful in addressing this question. It would be strange indeed if screening-off were useful in the first context (genic selectionism) but not the second (levels of selection).

Sober's critique of Brandon's views on levels of selection focuses on group selection. This is unfortunate since Sober seems to neglect the distinction between group growth (the rate of reproduction of individuals comprising the group) and genuine group reproduction (see Brandon 1986; 1990, 123–127). Thus he thinks it is a matter of indifference as to how we measure group adaptedness, either in terms of group growth or group reproduction (see Sober 1992, 144). In what follows we will disambiguate Sober's remarks on group adaptedness, interpreting them exclusively in terms of expected group reproductive success (but see fn. 2).

Sober starts by *misstating* Brandon's characterization of group selection. According to Brandon, "[G]roup selection occurs if and only if (1) there is differential reproduction of groups; and (2) the group phenotype screens off all other properties (of entities at any level) from group reproductive success" (1990, 87–88). Compare this to Sober:

> Brandon's proposal ([1982] 1984, 137; 1990, 87) is that there is group selection—that is, selection at the level of the group—precisely when two conditions are satisfied. The first is that there are different groups that reproduce differentially. The second is that for each group G, and for any set O of propositions that characterize the organisms in G,
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> $$\text{Exp}\ (G/G\text{'s level of adaptedness is } n\ \&\ O) = \text{Exp}\ (G/G\text{'s level of adaptedness is } n) \neq \text{Exp}\ (G/O) \qquad \text{(B)}$$
>
> (1992, 144–145)

(where Exp (G/X) is G's expected number of offspring groups conditioned on X). The crucial difference between Sober's characterization and the genuine article is that Brandon claims in (2) that group *phenotype* screens off properties at other levels whereas Sober puts this in terms of group *adaptedness values*. The trouble with Sober's formulation (B) is that the equality in it could not help but be true; it is definitionally true, whereas what we need in the first clause of a screening-off statement is a contingently true equality. This follows from Salmon's (1984) view that explanatory power is gained by *causally relevant* partitions of the original reference class. (In Salmon's [1971] earlier work, where he tried, ultimately unsuccessfully, to completely explicate causation in terms of statistical relevance, only statistically relevant partitions would be candidates for explanatory status.) Thus partitioning the reference class in terms definitionally related to the explanandum is disallowed in screening-off.[1] Brandon (1982) makes the mistake repeated in Sober's (B), but that is corrected in Brandon (1988, 1990) where he provides the needed contingency by switching from *group adaptedness value* to *group phenotype*.

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[1] For instance, we would not allow "shows George Washington's face" as a potential screener off of anything with respect to the outcomes of tosses of a U.S. quarter, even though Pr(H, *G. W.*'s face shows & the coin was tossed on a Tuesday) = Pr(H, *G. W.*'s face shows) ≠ Pr(H, the coin was tossed on a Tuesday) where "H" stands for heads.

The former is definitionally equivalent to expected group reproductive success whereas the latter is not. Whether group phenotype screens off some conjunction of properties of component organisms from group reproductive success is precisely the question at issue when determining if selection is occurring at the group level.

Sober offers an example that he thinks shows that Brandon's characterization of group selection will not work. We think the example is too thinly described to make any determinate judgement. The example concerns fertility selection where the expected reproductive success of a mating pair depends on the exact combination of maternal and paternal genotypes. This is an example of frequency-dependent selection. It is plausible that all cases of group selection are cases of frequency-dependent selection, but not vice versa.[2] Similarly, Brandon (1990, 105–109) has shown that all cases of group selection are cases of individual selection in heterogeneous selective environments, but not vice versa. When a population is structured into groups within which there are fitness affecting interactions that make fitness frequency-dependent, and there is variation in the relative frequency of the interacting types among groups, then there is the *potential* for group selection. Whether this potential is realized depends on whether the among-group selective heterogeneity results in differential group *reproduction*. This could happen in a case of fertility selection and be consistent with Sober's description. (If the groups simply grow at different rates and never reproduce, then group selection does not occur. For discussion see Brandon 1990, 109–127. This is a point over which Brandon and Sober disagree, see e.g., Sober 1984, 318, 330; and 1992, 144.)

Thus Sober's conclusion that his example is obviously not group selection is reached too quickly. For instance, are these organisms monogamous or polygamous? If monogamous, then we think it is a genuine case of group selection where the groups are the mating pair. If polygamous, then, although Sober has not described his example fully enough to tell, there is the potential for group selection where in this case the groups are demes. That is, we can construct scenarios consistent with Sober's description in which genuine group selection occurs—for example, when successful group fission (reproduction) is a probabilistic function of group size at the end of the season and group size is, in turn, a function of the initial distribution of genotypes in the group.

The relation between individual and group selection and the concept

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[2] See Uyenoyama and Feldman (1980, 395). They define a group as "the smallest collection of individuals within a population defined such that genotypic fitness calculated within each group is not a (frequency-dependent) function of the composition of any other group". Thus a group is the smallest unit within which there are fitness affecting interactions and beyond which there are none.

of selective environments within which selection occurs are too complex to be dealt with here. (On the notion of the selective environment see Antonovics et al. 1988, as well as Brandon 1990, chap. 2. For some exciting empirical work employing this concept see Stratton 1992, 1994.) They are also too complex to be dealt with responsibly by means of underdescribed examples and unsupported intuitions. Finally, in ostensibly criticizing Brandon's (1990) book that devotes an entire chapter to explicating an abstract and technical concept of *selective environment* (as distinct from the *external* and *ecological environments*) and explaining its relevance within the theory of natural selection, Sober cannot counter Brandon's claim that (*simple* as opposed to *compound*) selection can only occur within common selective environments by simply saying, "Every two organisms (or groups) live in environments that are similar in some ways but dissimilar in others" (1992, 147). Again, this is just an equivocation here between the technical notion of selective environment and the commonsense notion of environment.

In this discussion we have responded to Sober's criticisms of Brandon's use of screening-off in the philosophy of biology. We have found that some are based on misunderstandings and misinterpretations; they, not surprisingly, fall short of their mark. Others, it seems, are based on a deep, not fully articulated, disagreement between Brandon and Sober. Brandon's position is committed to the appropriateness (at least in this biological context) of the ontic conception of explanation, and so committed to an objective interpretation (more specifically, the propensity interpretation) of the probabilities involved in screening-off. Some of Sober's objections (certainly those covered in sec. 2, and probably the major one covered in sec. 1) are based on an epistemic conception of explanation and, correspondingly, an epistemic or subjectivist interpretation of probability. Although our philosophical prejudices are probably clear, these issues are deep and unresolved, and are, we believe, the principal locus of the disagreement between Brandon and Sober.

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