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Thinking about evolutionary mechanisms: natural selection

Robert A. Skipper Jr.^a, Roberta L. Millstein^b

^a *Department of Philosophy, ML 0374, University of Cincinnati, Cincinnati, OH 45221-0374, USA*

^b *Department of Philosophy, California State University, East Bay, CA 94542-3042, USA*

Abstract

This paper explores whether natural selection, a putative evolutionary mechanism, and a main one at that, can be characterized on either of the two dominant conceptions of mechanism, due to Glennan and the team of Machamer, Darden, and Craver, that constitute the ‘new mechanistic philosophy’. The results of the analysis are that neither of the dominant conceptions of mechanism adequately captures natural selection. Nevertheless, the new mechanistic philosophy possesses the resources for an understanding of natural selection under the rubric.

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1. Introduction

This paper explores whether natural selection—a putative evolutionary mechanism, and a main one at that—can be adequately characterized under the rubric of the ‘new mechanistic philosophy’. What we call the new mechanistic philosophy is comprised of two dominant conceptions of mechanism, one due to Glennan

E-mail addresses: robert.skipper@uc.edu (R.A. Skipper Jr.), roberta.millstein@csueastbay.edu (R.L. Millstein).

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(1996, 2002a, 2002b) and the other due to the team of Machamer, Darden, and Craver (2000). The new mechanistic philosophy has the broad aim of building a philosophical framework for understanding the nature and role of mechanisms in science. And our aim is to determine whether natural selection can be adequately described within that framework. We argue that it cannot. Indeed, we argue that neither of the two main conceptions of mechanism adequately captures natural selection as a mechanism.

We begin in Section 2 by discussing the mechanism of natural selection and presenting it in a schematic form ripe for probing the new mechanistic philosophy. In Section 3, we explicate the dominant conceptions in the new mechanistic philosophy, delineating three key differences between them. These differences feed our analysis of natural selection on the new mechanistic philosophy that we present in Section 4. The results of Section 4 are largely negative. Nevertheless, on the basis of our results, in Section 5 we conclude the paper by sketching directions for further work under the rubric of the new mechanistic philosophy.

2. Natural selection

We recognize that natural selection is not the sole mechanism of evolution. Indeed, textbook accounts of evolution typically delineate four evolutionary mechanisms: (1) natural selection, (2) random genetic drift, (3) mutation, and (4) gene flow or migration. We limit our attention in this paper to natural selection for two related reasons. First, natural selection is the apotheosis of the four mechanisms. Second, because of the first, natural selection has received the most philosophical attention of the four mechanisms.

Discussion of natural selection as a mechanism is pervasive in evolution. For example, Roughgarden, in discussing Darwin's contribution, states, 'Darwin's second proposition is that the *mechanism*, or driving force, of evolution is natural selection' (Roughgarden, 1996, p. 26; *italics added*). Futuyma, introducing evolutionary biology, says, '[t]he several *mechanisms* of evolution include natural selection, which accounts for the diverse adaptations of organisms to different environments' (Futuyma, 1986, p. 7; *italics added*). And Hartl and Clark say, '[t]he process of evolution includes all *mechanisms* of genetic change that occur in organisms through time, with special emphasis on those *mechanisms* that promote the adaptation of organisms to their environment or that lead to the formation of new, reproductively isolated species' (Hartl & Clark, 1989, p. 329; *italics added*); it is clear that they are talking about natural selection here, among other things.

Actually, evolutionary biologists call natural selection, and the other evolutionary mechanisms, many things, which they all seem to think amount to the same thing. Natural selection is a 'cause,' a 'force,' a 'process,' a 'mechanism,' a 'factor'. Sometimes, natural selection is called a 'principle' or a 'concept,' but when the explication continues, cause, force, or mechanism talk is apparent. We think there is no question that contemporary evolutionary biology exemplifies the view that natural selection is

a mechanism. The interesting and harder question to answer is philosophical, namely, ‘What is the nature of the mechanism of natural selection?’

The schematic of natural selection in Figure 1 below sets out the mechanism as a chain of temporal steps or stages laying bare the causal crux of selection, that is, the essence of Darwin’s ‘struggle for existence,’ and its downstream effects.¹ The result is as follows: in natural populations there exist organisms which vary according to certain properties (stage I in Figure 1). Organisms interact with their environments and that interaction can be affected by the properties the organisms possess (stage II). The properties of organisms affect their chances for survival and reproduction in a variety of ways, and these chances are measured relative to the chances of survival and reproduction conferred on other organisms by their properties. Assuming the properties, or traits, are heritable, those organisms whose chances at survival and reproduction have been increased by their interaction with their environments have a tendency to leave more offspring with the same or similar properties in future generations. The opposite is true for organisms that have had their survival and reproductive chances decreased by their interactions with their environments (stages III–IV). Over time, the properties that increased chances of survival and reproduction for their possessors tend to be more prevalent in the population (stage V). And after many generations, the vast majority of the members of the population have that property (stage VI). This may lead to lineage adaptation (stage VII).

As an illustration based on a gloss of the familiar case of Darwin’s finches, consider the following instantiation of the schematic in Figure 1. There exists a population of finches, *Os*. The finches vary according to their beak length *T*, the form of a trait that is heritable. And the finches are in a rocky environment *E* where there is a critical factor, *F*—variously shaped edible seeds varying in availability. Notice that the critical factor *F* in conjunction with differences in *T* is what sets up the selective interaction. Certain beak lengths enable some of the finches to obtain seeds that other finches, lacking the appropriate beak length, are unable to obtain. This constraint on environmental resources that leads to a struggle for existence and a check on the population is the interaction step of the schematic. Given the initial conditions and the causal interaction between the environment and the finches, we expect various downstream effects. That is, we expect differential survival and reproduction, and the other stages described in Figure 1, based on the ways in which the critical factor *F* and trait form *T* affects the interaction of the finches in environment *E* with critical factor *F*.

To accompany the schematic representation of natural selection in Figure 1—the two must be considered together—we provide the directed diagram in Figure 2. The purpose of the diagram in Figure 2 is to lend a strong sense of dynamics to the stages of natural selection delineated in Figure 1 and, more importantly, to make clearer how we understand the way the mechanism works; in fact, how evolution by natural

¹ Our schema is a direct descendant of that found in Darden & Cain (1989) and Skipper (1999, 2001). For alternative conceptions, see Brandon (1980), Dawkins (1989), Hull (1988), Hull, Langman, & Glenn (2001), Kitcher (1989), Lennox & Wilson (1994), Lewontin (1970), and Sober (1984).

Structure:

I. Initial conditions

1. A population of *O*s exist.
2. *O*s vary according to forms of *T*, which are heritable.
3. *O*s are in environment *E* with critical factor *F*.

II. Interaction

1. *O*s in virtue of the varying forms of *T* interact differently with environment *E*.
2. Critical factor *F* affects that interaction.
3. This may lead to

III. Effects (1)

1. differential survival rates of *O*s across forms of *T* in *E*.
2. This may lead to

IV. Effects (2)

1. differential reproductive rates of *O*s across forms of *T* in *E*.
2. This may lead to

V. Effects (3)

1. differential representation in the population of *O*s across forms of *T* in *E*.
2. This may lead to

VI. Effects (4)

1. the predominance of *O*s with a certain form of *T* over other forms of *T* in *E*.
2. This may lead to

VII. Effects (5)

1. adaptation of the lineage with respect to *T* in *E*.

Filling instructions:

- '*O*' is to be replaced by the name of some organism
- '*T*' is to be replaced by some determinable organismic trait
- '*E*' is to be replaced by the description of the environment of '*O*'
- '*F*' is to be replaced by the description of a critical factor in '*E*'

Fig. 1. A schematic of the process of natural selection. The process of natural selection is represented as a series of stages (I–VII). The accompanying 'Filling instructions' aid instantiation of the schematized mechanism by indicating how to 'fill in' the variables in the schema. Note that with each 'iteration' (see text) the variables may change.

selection works. The solid arrow linking stage (V) to stage (II) represents that stages (II–V) may reiterate prior to moving to stage (VI). A population will have a preponderance of organisms with a certain trait form (stage VI) only after many iterations of natural selection and its immediate effects on rates of survival and reproduction among the organisms (stages II–V). Now, to get to stage (VII) from stage (VI), an iteration through all preceding stages requires a change in stage (I), such as a change in the environment or a mutation. The arrow linking stage (VI) to stage (I) represents

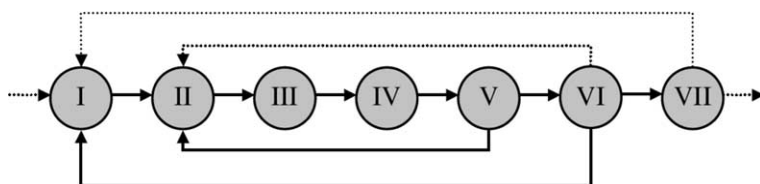


Fig. 2. A directional schematic diagram of the mechanism of natural selection. The circles labeled with Roman numerals correspond to the stages delineated in Figure 1. Each stage is linked by a solid or dashed causal arrow to represent productive continuity between the stages.

this iteration. The dashed arrow from stage (VI) back to stage (II) represents that a population at stage (VI) may be in stasis with one type predominant, continuing to pass through stages (II–V). The dashed arrow from stage (VII) to stage (I) represents that an adapted lineage may start the process of evolution by natural selection over again as a result of a change in initial conditions (stage I). Or, as is represented by the dashed arrow leading out of stage (VII), other mechanisms may follow. The dashed arrow leading into stage (I) represents that there are mechanisms leading to the formation of the initial conditions in stage (I).

Now, in our mechanistic representation of natural selection, we have made every effort to respect the population-level description that current population genetics theory embodies (Millstein, unpublished). To that end, what we make clear in our schematic of natural selection is the way in which populations enter into causal interactions with their environments to produce relative fitness changes, where relative fitness is a measure of the relative abilities of organisms of different types (specifically, genotypes) to reproduce. Ultimately, while we realize that our schematic of natural selection is not representative of population genetics theory, where the theory is a family of mathematical models, we are convinced that to a significant extent it captures the *phenomenon* that population genetics theory models. And, further, we think that the schematic, as an abstract description of natural selection that lays bare its causal crux, provides the best chance for making progress toward understanding natural selection as a mechanism in particular and toward understanding the nature and role of mechanisms in science in general.

In the discussion that follows, we return to many of the issues broached in the present section, and in particular we make use of the instantiation of the schematic in Figure 1. In the next section, we set out what we take to be the new mechanistic philosophy with the aim of analyzing the mechanism of natural selection as we have presented it here under the philosophy's rubric.

3. The new mechanistic philosophy

Two conceptions of mechanism are at the forefront of the new mechanistic philosophy, one developed by Glennan, and the other by the team of Machamer,

Darden, and Craver (hereafter MDC) (Glennan, 1996, 2002a, 2002b; MDC, 2000). In the present section, we set out Glennan's and MDC's conceptions of mechanism to set the stage for our analysis of natural selection as a mechanism in Section 4 below. Specifically, we exposit Glennan's and MDC's conceptions of mechanism delineating what we take to be three key differences that feed our analysis of natural selection on the views.

Glennan's original conception of mechanism was motivated by the idea that a mechanism is a complex-system whose parts interact to produce a behavior (Glennan, 1996; cf. Bechtel & Richardson, 1993, p. 17). Such mechanisms Glennan calls 'things', by which he seems to mean 'complex-systems': '[C]omplex-system mechanisms are *things* (or objects)' (Glennan, 2002b, p. S345; italics in original). Moreover, he maintains, '[m]echanisms in the sense I have described them here are *things*—that is, systems that are collections of parts' (Glennan, 2002a, p. 128; italics in original). Glennan has modified his original conception of mechanisms as complex-systems (hereafter 'systems-mechanisms') over the course of his published work on the topic; his most recent conception is as follows:

A mechanism for a behavior is a complex system that produces that behavior by the interaction of a number of parts, where the interactions between parts can be characterized by direct, invariant, change-relating generalizations.² (Glennan, 2002b, p. S344)

The key example Glennan uses to explicate the conception of mechanism above is the toilet, a system whose collection of interconnected parts interact to replace waste and water. Many biological examples are, *prima facie*, likely to fit Glennan's systems-conception as well. The heart, for example, is a system whose collection of interconnected parts interacts to pump blood.

Glennan distinguishes between systems-mechanisms and mechanisms as 'processes' (hereafter 'process-mechanisms'), which he derives from the work of Salmon and Railton (*ibid.*, p. S343). For Glennan, a process-mechanism is a unique causal chain of events, that is, a singular sequence of possibly 'interlocking' events of 'arbitrary complexity' (Glennan, 2002a, p. 128). Glennan introduces this conception via a request for a description of what he thinks is just such a mechanism, 'What is the mechanism that led to the outbreak of World War I?' According to Glennan, this request concerns the causal nexus in which a particular event, here the assassination of Archduke Ferdinand, can be said to cause another particular event, that is, the outbreak of World War I.

Glennan says little more about what constitutes process-mechanisms; his focus is on systems-mechanisms. Indeed, process-mechanisms are primarily described by what they are *not*. Process-mechanisms do not form a stable enough configuration to be called a system, they do not have stable dispositions that can manifest

² Glennan's (1996), p. 52, original conception relied on 'direct, causal laws' to govern interactions. Due to well known problems explicating the nature of such laws, Glennan has more recently relied on Woodward's (2000, 2003) explication of 'direct, invariant, change-relating generalizations'. For our purposes, nothing hinges on Glennan's move from laws to generalizations.

themselves at more than one time and place, and they do not consist of types with many different tokens (Glennan, 2002b, p. S345). Furthermore, they do not reliably produce behaviors, that is, they are not ‘robust’ (Glennan, 2002a, p. 128).

In addition, it is not at all clear that much of anything that Glennan says about systems-mechanisms applies to process-mechanisms. One crucial point concerns what connects the stages in a mechanism that produce change from the beginning of the chain to the end (what MDC, 2000, p. 3, usefully call ‘productive continuity’). In a systems-mechanism, ‘interaction’ does this work. For Glennan, an interaction is ‘an occasion on which a property change in one part brings about a property change in another part’ (Glennan, 2002b, S344). Now, process-mechanisms for Glennan may involve systems-mechanisms, although processes are not themselves systems. So, it is plausible that the parts interacting in a process are the parts of the systems involved in the process. In the World War I example, then, the key event of the assassination of Archduke Ferdinand will be unpacked so that the relevant systems with parts interacting are productive of the change leading to the outbreak of the war. Alternatively, the event itself (i.e., the higher level phenomenon) may be what is productive of change. Ultimately, the issue is not clear; a fuller explication of the nature of a process-mechanism is required (cf. work on causal-mechanical explanation by Salmon, 1998; Woodward, 2003).³

Shortly after Glennan’s (1996) conception of mechanism, MDC defended their own conception of mechanism:

Mechanisms are entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions. (MDC, 2000, p. 3)

This brief characterization is fleshed out via the mechanisms of neuronal depolarization and the mechanism of protein synthesis. The MDC conception of mechanism has been developed further, principally by its inventors (e.g., Craver & Darden, 2001; Darden & Craver, 2002).

The ‘activities’ in mechanisms are the producers of change, and the ‘entities’ are what engage in those activities. The specific activities that occur, for example, geometrico-mechanical, electro-chemical, energetic, and electro-magnetic, require that entities have certain, relevant properties. Entities and their activities are key to MDC’s conception of mechanism; they account for productive continuity through mechanisms. The ‘organization’ of mechanisms is provided by the precise staging or continuity of the entities and activities: ‘[E]ntities often must be appropriately located, structured, and oriented, and the activities in which they engage must have a temporal order, rate, and duration’ (MDC, 2000, p. 3). This continuity is what makes for ‘regular,’ productive change from beginning to end in a mechanism:

³ Glennan is currently working on developing the concept of a process-mechanism as a process (personal communication, RM).

‘[M]echanisms are regular in that they work always or for the most part in the same way under the same conditions’ (ibid.).

There are other features of the MDC conception of mechanism and its representation. ‘Start-up’ and ‘termination’ conditions are idealized (ibid., p. 11). A given start-up condition in a mechanism is identified as a time-slice of a mechanism, and may be the result of prior processes. Similarly, termination conditions are identified as a time-slice of a mechanism, with the mechanism itself continuing, or the termination state being part of the start-up condition of another mechanism. In addition, for MDC, mechanisms have ‘bottom out’ points that are idealized relative to some field of inquiry (ibid., p. 13). For instance, molecular biologists typically bottom out their mechanisms at molecules, without consideration of quantum level entities and activities. Finally, mechanisms on the MDC conception are represented by ‘mechanism sketches’ and ‘mechanism schemata’ (ibid., pp. 15–16).⁴ Mechanism schemata are abstract descriptions of a mechanism to be filled in with descriptions of known component parts. The examples MDC use are diagrammatic, but there is no reason to think that a mechanism schema must be a diagram. A mechanism sketch is a more incomplete abstract representation of a mechanism. Notice that the schematic representations of natural selection in Section 2 reflect MDC’s idea of a mechanism schema. A number of MDC’s insights in their development of the idea are exemplified in [Figures 1 and 2](#) above, for example, there are start-up and termination conditions, each is an abstraction, and one is diagrammatic. Yet, we hesitate to call our schematic representations ‘mechanism schemata’ because, as we will see below, they are not MDC-type mechanisms.

To sum up, from the preceding discussion of Glennan’s and MDC’s conceptions of mechanism, we draw out the following three key differences between them. First, Glennan explicitly distinguishes between systems-mechanisms and process-mechanisms. MDC offer a univocal conception. Second, Glennan relies on the notion of interaction to account for productive continuity through mechanisms. MDC reject the interactionist perspective for their dualistic approach emphasizing entities and activities of mechanisms to account for productive continuity. Finally, Glennan uses direct, invariant, change-relating generalizations to characterize the regularity of mechanisms (cf. [Glennan, 1997](#) on stochastic mechanisms). MDC hold to an apparently looser notion of regularity, in which mechanisms are regular if they ‘work always or for the most part in the same way under the same conditions’ ([MDC, 2000, p. 3](#)).

Against the background of the preceding discussion of the dominant approaches in the new mechanistic philosophy, we argue in the next section that neither Glennan’s nor MDC’s conceptions of mechanism adequately capture the mechanism of natural selection. We now turn to an analysis of natural selection on the dominant approaches of the new mechanistic philosophy.

⁴ Skipper (1999) coined the phrase ‘mechanism schema’. However, Machamer, Darden, & Craver (2000) develop the concept more fully than Skipper does.

4. Glennan, MDC, and natural selection

In this section, we argue that natural selection is not organized in the ways Glennan or MDC argue, that productive continuity between its stages is captured neither by Glennan's 'interactions' nor by MDC's 'entities' and 'activities,' and that natural selection is not 'regular' in the way that MDC claim.

However, before we proceed, we must consider a preliminary issue, namely, whether natural selection broadly fits either of the two types of mechanism that Glennan distinguishes (systems-mechanisms and process-mechanisms). We argue that selection fits neither, but Glennan's account of process-mechanisms can be eliminated from consideration at the outset.

On Glennan's account, a process-mechanism is a unique causal chain of events, such as the mechanism that led to the outbreak of World War I. However, natural selection is by no means a unique causal chain of events. To be sure, the specific causal chain, or string of temporal, causal stages, that led to the predominance of a specific property of a specific population of finches is unique. So, it is proper to ask, 'What was the mechanism that led to this population of finches having this beak trait?' However, it is also proper to ask the more general question, 'What is the mechanism that leads to populations of organisms having some predominant trait?' The first request demands a unique causal chain. The second demands a type of causal chain. The schematic in [Figure 1](#) satisfies this latter demand by abstracting away from a unique causal chain and laying bare the key elements of the mechanism. According to Glennan, a process-mechanism is not a type with particular tokens. Yet our natural selection schematic describes a type; filling out the schema with particular values yields selection tokens.

Natural selection is a pervasive mechanism that explains adaptations in the living world; it is not merely the explanation of some specific past adaptation event. Moreover, previous philosophical work indicates that the selection mechanism, suitably abstracted, accounts for such phenomena in multiple domains, for example, evolutionary biology, immunology, and, speculatively, neurobiology (e.g., [Darden & Cain, 1989](#); [Hull, Langman, & Glenn, 2001](#); [Skipper, 1999](#)). Since natural selection is not a unique causal chain of events—since it is a type with tokens—it does not fit Glennan's brief characterization of a process-mechanism. Thus, in the discussion that follows, we focus on Glennan's systems-mechanism conception.

MDC do not distinguish between systems-mechanisms and process-mechanisms as Glennan does; they offer a univocal alternative conception of mechanism. We think that MDC's conception of mechanism can capture the pervasive mechanisms in molecular and neurobiology on which their attentions are focused. But they suggest that their approach may apply to other scientific fields ([MDC, 2000, p. 2](#)). Our purpose, of course, is to determine whether evolutionary biology is a field in which either the MDC or the Glennan mechanism conception applies. We have said that neither applies. Our method is to try to fit our schematic mechanism to Glennan's and MDC's conceptions of mechanism, focusing on what we take to be the causal crux of selection, stages (II–V) in [Figures 1 and 2](#).

4.1. Organization

We first consider the question of the ‘organization’ of a putative mechanism. The claim that mechanisms are organized implies (1) that mechanisms are comprised of various elements and (2) that those elements are structured in some way. We first explore (1), for Glennan and MDC in turn, and then address (2).

As we noted in Section 3 above, Glennan is unclear about his understanding of a systems-mechanism, treating ‘system’ as synonymous with ‘thing’ or ‘object’. Nevertheless, what Glennan seems to be getting at is the idea that mechanisms are complex-systems decomposable into their parts, and that these parts interact in certain, reliable ways to produce a given behavior (Glennan, 1996, p. 52). Is natural selection such a system? *Prima facie*, it would not seem to be: is there any sense to decomposing natural selection into its putative parts? What would those parts be? The organisms? Their traits? The environment? Specific aspects of the environment? If natural selection can be understood in terms of parts, clearly it will not do so as neatly and tidily as a toilet, Glennan’s favorite example. Settling the issue of whether natural selection is organized in accordance with Glennan’s conception of a systems-mechanism requires further exploration of the details of Glennan’s account.

One aspect of Glennan’s view that has remained constant over time is his insistence that a mechanism is always *for* a behavior; that is, when we identify a mechanism, we always identify what that mechanism does (Glennan, 1996, 1997, 2002a,b). This seems relatively unproblematic for the mechanism of natural selection; we might, for example, understand stages (III–VII) as things that natural selection does. That is, natural selection may produce differential survival rates of *O*s across forms of *T* in *E*, differential reproductive rates of *O*s across forms of *T* in *E*, differential representation in the population of *O*s across forms of *T* in *E*, or lineage adaptation with respect to *T* in *E*.

Glennan has also been consistent in his view that systems-mechanisms are complex-systems composed of ‘parts’. However, his view of what constitutes a ‘part’ has changed over time. Most recently, Glennan (2002a, p. S345) says that the properties of a part must be stable in the absence of interventions, or, as he subsequently clarifies, the complex of objects must form a stable enough configuration to itself be called an object. Moreover, his recent work holds that parts can ‘generally’ be spatially localized (*ibid.*, p. S344), and his assertion that a mechanism’s behavior is ‘the set of dispositions which the system has in virtue of the arrangement of and connections between its parts’ (Glennan, 2002b, pp. 126–127) suggests that he thinks of parts strictly physically. (It is puzzling to speak of the arrangement of and connections between *non-physical* parts.)

Given Glennan’s current conception of ‘part’, can we describe the parts of a natural selection mechanism in the way that we can describe the parts of a toilet? One possibility is that the organisms and the environment are parts. Assuming that an environment can be considered to have stable properties as required on Glennan’s account (an assumption that depends crucially on the length of time at issue), a question arises as to whether the environment is one part or many. And if many, how many? Do we consider weather to be a part? Is each seed in the finches’ environ-

ment—in our gloss on the finch case—a part? Is water another part? Glennan (1996) says that there may be more than one way to split a system into parts, but he does not tell us how this should be done. With an entity as diverse and diffuse as the environment, this is a nontrivial issue. Turning to organisms, at first glance, they appear to be easier to characterize as parts; they are often (but not always) identifiable as individuals, they have relatively stable properties in the absence of interventions, and they do have a spatial location, although do not necessarily have any particular spatial location.

Another possibility is that populations are parts of the natural selection mechanism. But again, we run into the immediate problem that a population does not have stable properties, as required by Glennan's account. Indeed, the 'behavior' of the natural selection mechanism is to change the population, which raises a further problem. A mechanism provides an explanation for its outcome. Citing the same entity (albeit, a changed entity) serving as a part of a mechanism and as its outcome conflates the *explanans* and the *explanandum*. It flies in the face of Glennan's (1997, p. 510) view that when one describes a mechanism, one must first 'describe the "external" behavioral dispositions of the mechanism—what the mechanism does' and then 'describe the "internal" structure of the mechanism which underlies the outward behavioral dispositions—how the mechanism works'. If populations are both parts of the mechanism and the subject of the mechanism's behavioral disposition(s), then populations are both internal and external, which is incoherent.

In short, there are difficulties in determining how, on Glennan's account, a mechanism is comprised of its elements. MDC are more explicit about the elements of a mechanism. Their conception of mechanism includes both entities (with their properties) and activities. In our gloss on the finch example, the most obvious entities are the finches, with beak length being the property of interest. What, then, are the activities of these entities? That is, what are the activities that account for the productive changes from one stage of the mechanism to another (the causal arrows in Figure 2). The finches are engaging in survival activities (such as feeding) and reproduction activities (mating). Perhaps these might be broadly characterized as MDC's 'geometrico-mechanical' or 'energetic' type activities. And these activities are indeed producers of change, in accordance with MDC's account; the feeding (survival) activity increases the chances of the reproducing activity (mating), whereas less feeding activity may decrease the chances of the reproducing activity. So far, so good, even if this presentation is somewhat forced. This is similar to treating organisms as parts for Glennan.⁵

However, a difficulty arises in trying to see how, for natural selection, these entities and activities are 'organized in such a way as to be productive of regular changes' (MDC, 2000, p. 3), and this raises the issue of the second aspect of organization, namely, the idea that elements of the mechanism are structured in some way. Recall that on MDC's account, the entities 'often must be appropriately *located, structured, and oriented*, and the activities that they engage in must have a *temporal order, rate,*

⁵ But see the related discussion of 'productive continuity' below.

and *duration*' (ibid.; italics added). Glennan makes a similar, albeit weaker, claim, namely, 'mechanisms are systems consisting of *relatively stable configurations of parts* that give rise to robust behaviors which can be expressed by invariant generalizations' (Glennan, 2002b, p. S348; italics added).

Neither of these accounts of mechanism organization hold for natural selection. Consider the Grants' study of one species of Darwin's finches, the large cactus finch, *Geospiza conirostris* (Grant & Grant, 1989). According to the Grants, a geographical region that in one year is occupied by a male who sings one of the predominant song types may, in the next year, be occupied by a male who sings the other predominant song type (ibid., p. 242).⁶ This example shows that organisms need not be found in any *particular* location. Moreover, whereas in one year, 'song A' males spent more time feeding on cactus flowers and 'song B' males spent more time feeding on cactus pads on the ground, in a different year equal numbers were observed feeding on flowers, suggesting a change in *structure* and *orientation*. Grant and Grant found that, for the most part, the female *G. conirostris* can feed her fledglings or produce and incubate another clutch of eggs, but not both, and that 'resolution of the conflict varies annually' (ibid., p. 79). This is an example of how the activities of organisms do not have any *particular* temporal order. The Grants also found that the 'rate of clutch production is faster at some times than at others' (ibid., p. 77)—an example of how the activities of organisms do not occur at any *particular* rate. Finally, to take an obvious example, the finches differed in the length of their lives (ibid., p. 298), a variation in the *duration* of their activities.

All of these examples call into question the applicability of MDC's mechanism conception to natural selection. Indeed, they also call into question the applicability of Glennan's account; organisms that vary in their location and orientation do not have a 'stable configuration'. And we should not be surprised at the variability of finches and other organisms. Although there has been a great deal of controversy over the source of variation in natural populations, variation is a necessary condition for natural selection. This means that it is unlikely that natural selection has the degree of organization required by either MDC or Glennan.

But let us be clear. It may be possible to find a certain degree of organization among organisms. For instance, there may be certain preferred locations for nesting (although mutation or recombination within the population may change those preferences if they are genetic in origin). What we question is whether the degree of organization among organisms is *sufficient* to satisfy either MDC's or Glennan's account, although neither provides guidelines for measuring degrees of organization, so it is hard to say. However, there is a more important point to be made here. Even if we could determine that the organization of *G. conirostris* was sufficient to satisfy MDC's and Glennan's accounts, the organization of other species would be different. Other birds nest differently, feed differently, and mate differently. Of course, other organisms do not nest at all, and some do not mate at all (asexual reproducers). In other words, we can give no *general* account of organization in populations

⁶ Grant & Grant (1989) were exploring the possibility that the two song groups were incipient species.

undergoing natural selection. And if that is right, then there is no general mechanism, *sensu* MDC and Glennan, of natural selection to be found.

We suggest that a more appropriate way of understanding how natural selection is ‘arranged’ or ‘organized’ is implicit in our representation of it in Figures 1 and 2 above: natural selection is a series of *stages*. As Glennan makes clear, to articulate the toilet as a mechanism, one decomposes it into its discrete, component parts. The specific interactions of those parts, the handle, flapper valve, float valve, and so on produce the behavior of replacing waste and water in the bowl. The straightforward way to articulate natural selection as a mechanism is by explicating all of the *stages* integral to causing populations to change. The stages themselves are not parts in Glennan’s sense or entities in MDC’s sense. They are, instead, salient, if not idealized, *time-slices* of the process of natural selection. Each stage, for example, the selective interaction, changes in survival and reproductive rates, and so on is integral to a certain kind of change in populations, namely, adaptive change. To be sure, there are details to fleshing out the stages of natural selection that require describing organisms and their properties, environments with critical factors, survival and reproductive rates, and so on. But rather than these being understood as ‘parts’ (in Glennan’s sense) or ‘entities’ and ‘activities’ (in MDC’s sense) of the mechanism of natural selection, they go hand in hand with accounting for the stages of natural selection.

4.2. Productive continuity

Let us set aside the organization of the mechanism of natural selection for the moment and turn to whether MDC’s or Glennan’s conceptions of mechanism capture productive continuity in natural selection, or productive change between stages in natural selection. We think neither conception does so. We begin, as we did previously, with Glennan’s account.

The real heart of Glennan’s conception of a systems-mechanism is his understanding of ‘interactions’; interactions are how Glennan accounts for productive continuity in a mechanism. That is, the interactions between parts in a mechanism that provide for its robust behavior are what account for the way in which the mechanism’s parts produce that behavior. Indeed, explicit in our schematic representation of natural selection in Figure 1 is a reliance on a type of interaction (see stage II). But we think Glennan’s understanding of interactions fails to capture productive change in natural selection.

Recall that, for Glennan, an interaction is ‘an occasion on which a property change in one part brings about a property change in another part’ (Glennan, 2002b, p. S344). To an extent, it is plausible that Glennan’s ‘property change’ view of interaction captures productive continuity in natural selection. Consider the way stage (III) produces stage (IV), that is, the way changes in survival rates change rates of reproduction. If one permits the population of finches, *O*, to be a part in the natural selection mechanism, then it is plausible that the change in the survival-rates property of some finches with some form of trait *T* brings about the change in the reproductive-rates property of those finches. Indeed, this way of capturing

productive continuity can be extended through stages (V–VII), allowing that the changes in reproductive rates brings about changes in representative numbers of finches with some form of trait T (stage V), and then a preponderance of those finches (stage VI), and finally lineage adaptation (stage VII).

Now consider whether the idea that a property change in one part of a mechanism may bring about a property change in that same part violates Glennan's account of interaction. Taken at face value, it does. The intuition Glennan is getting at is that an interaction is between two discrete objects. Yet, it is clear that in natural selection, changes in one property of a population may change another property in the same population. But perhaps that is not a crucial point. What is more important to notice, in our view, is that the *interaction* is between the population and the environment, but there is not a property *change* in the environment that brings about a property change in the population.

As is explicit in our schematic representation of natural selection in Figure 1, differences in the abilities of finches with varying forms of some trait T in environment E with critical factor F affect the survival and reproductive rates of those finches in that environment. That is, what does the 'bringing about' in natural selection, namely, what is at its causal crux, are the relevant differences between organisms against the background of their environment. Glennan's account of interaction as property changes between parts does not capture the dynamics, or the productive continuity, between stages in natural selection. And this is because Glennan's understanding of interactions does not capture the ways in which differences among organisms in a population may affect the ways in which that population *interacts* with its environment.

MDC's conception of mechanism does not fare any better. As we have seen, 'entities' and their 'activities' account for productive continuity in MDC-type mechanisms; activities in mechanisms are the producers of change, and the entities are what engage in those activities. Recall further that MDC identify four types of activities, namely, geometrico-mechanical, electro-chemical, energetic, and electromagnetic. Above, we intimated that, on the face of it, MDC's distinction between entities and activities captures productive continuity in natural selection for beak length in finches. The entities are easy enough to identify; these are organisms (groups, populations). And the activities are, broadly, survival-activities (feeding) and reproduction-activities (mating). However, consideration of a gloss on another well worn example of natural selection, namely, Kettlewell's peppered moths (see Rudge, 1999 for a critical interpretation), indicates otherwise.

On our Figure 1 schematic of natural selection, the initial conditions consist of a population of moths, O , varying in color (dark or light), T , in an environment, E , where there is a greater preponderance of dark backgrounds as compared to light, where the critical factor, F , is a predator that has difficulty spotting the moths when they are against similarly colored backgrounds. The critical factor and moth coloration affect the way the moths interact with their environment because the darker moths are camouflaged against the more prevalent dark backgrounds, making it easier for the moths to escape predating birds and increasing their survival chances. However, while we can specify the relevant organisms, the moths, as the entities,

we cannot specify the relevant activities. Being camouflaged in the way that the moths are is not an activity. In fact, many defensive selection mechanisms are passive in this way. Being poisonous, or having protective coloration are other examples of passive properties that nonetheless crucially affect the selective interaction. So, we cannot specify activities for the peppered moth case, as we could for the finch case.

Perhaps, however, we have not identified the entities correctly. That is, perhaps we have not identified what Darden (this issue) calls the ‘working entities’ in the mechanism. Perhaps in the peppered moth case it is not the moths that are the working entities (since, with respect to the property under consideration, they do not engage in activities productive of change), but rather the moths’ predators, which *do* engage in activities. This suggestion raises yet another difficulty, which can be seen by comparing the finch example to the moth example. In the finch case, the working entities are the finches, and the finches are what selection is acting on; they are the locus of the selective interaction. The seeds, which are the critical factor in the environment, are passive. However, in the moth case, if we were to take this new suggestion, the working entities are the predators, which comprise the critical factor, and what are selected, the moths, are passive (with respect to the selective interaction). Differently put, what is selected can be active *or* passive, and likewise, what causes the selection (the critical factor) can be active *or* passive. We cannot claim that the selection mechanism always has the same working entities (or the same kind). Thus, under the assumptions in force here, providing a univocal mechanism for natural selection on MDC’s account is unworkable.

The upshot of the preceding critical points is that MDC’s primary mechanism concepts, entities and activities, do not *get at* natural selection. Again, consider the finch case. It is true that finches are entities and that they engage in activities such as feeding (surviving) and mating (reproducing). The problem is that the activities of surviving and reproducing do not constitute selection. Differently put, the ways in which the finches and moths engage in survival and reproductive activities are elemental of selection. But just enumerating those entities and activities does not result in an articulation of the mechanism of natural selection. Because natural selection lacks the regularity and, in particular, the organization that are part and parcel of mechanisms on MDC’s view, we result in an articulation only of the life history of a population: Organisms are born, they eat, they mate, they die. Had Darwin’s *On the origin of species* announced that organisms engage in activities that allow them to survive and reproduce, he would have said nothing that was not already understood. Selection is not merely, if not something other than, the activities of survival and reproduction engaged in by entities. For these same reasons, we reject the idea that organisms can serve as ‘parts’ of a natural selection mechanism under Glennan’s conception of a systems-mechanism. Natural selection is likewise not merely the result of *interactions* between organisms.

4.3. Regularity

Up to this point, we have seen that natural selection is not captured by Glennan’s or MDC’s conception of mechanism with respect to organization and productive

continuity. We consider here whether the mechanism of natural selection is ‘regular’ in the way that Glennan and MDC-type mechanisms are. We argue that Glennan’s notion of regularity, ‘direct, invariant, change-relating generalizations’, holds promise for capturing the way in which natural selection is regular. We argue that MDC’s view that mechanisms are regular in that they ‘work always or for the most part’ is too strong. We begin, again, with Glennan’s view.

In addition to claiming that interactions are occasions of property changes of parts in a mechanism, Glennan (2002b, p. S344) claims that interactions are governed by ‘direct, invariant, change-relating generalizations’. These generalizations, original with Woodward (2000), are what account for the regularity of a mechanism on Glennan’s view. In other words, and as we saw above, when Glennan says a mechanism is robust, or that the interactions between parts in a mechanism are robust, he means that those interactions, the behavior of those parts, conform to invariant generalizations (cf. Woodward, 2002). Without going into details orthogonal to our key goal, a generalization that is invariant is one that supports the relevant counterfactual truth claims. The notion of invariance enters via an operationalization of such counterfactuals: a generalization *G* relating some variable *X* to some variable *Y* describes a causal relationship between *X* and *Y* if *G* holds, or is invariant, under at least some (but not necessarily all) interventions or manipulations on *X* (Woodward, 2002, p. S370).

As we discuss below, we understand natural selection as a probabilistic phenomenon, indicating that the mechanism is stochastic.⁷ And by this we mean, roughly, that the various selective effects identified in Figures 1 and 2 are made more likely by their causes, but that they are not guaranteed by their causes (Millstein, 2002). It is not clear from Glennan’s (2002a,b) discussions whether he intends to capture this kind of stochastic causal relationship. However, we think Woodward (2003, pp. 61–65) does intend to capture this kind of stochastic causal relationship. Indeed, Woodward believes that it is crucial to capture the idea of a ‘contributing cause’, or just the sort of causal relationship that exists between stages in natural selection. Roughly, what Woodward, at least in part, wants to capture about causal relations is the nature and extent of the dependency between two putatively causally related variables. Woodward thinks his articulation of invariance under interventions, roughly characterized above, captures contributing causes. Suffice it to say, for our purposes, that we think Woodward’s understanding of generalizations that govern causal relations holds promise for understanding the ways in which the mechanism of natural selection may be said to be regular. The key is a proper account of probabilistic causal relations. To the extent that Woodward’s account is an advance on this front is the extent to which it captures the causal relations in natural selection.

With respect to regularity on MDC’s account, recall that [m]echanisms are regular in that they work always or for the most part in the same way under the

⁷ Glennan’s (1997) very brief characterization of stochastic/stochastic mechanisms or deterministic/stochastic mechanisms might, if elaborated, do a better job of addressing this aspect of natural selection.

same conditions' (MDC, 2000, p. 3). However, we see natural selection as probabilistic. Imagine an ensemble of one hundred populations of finches, all with the same population size, the same distribution of beak lengths, and all located in the same environment. Let the finches engage in their survival and reproduction activities, and then examine the distributions of beak length in the subsequent generation. In this thought experiment, we would not expect the same distributions of beak length in each of the one hundred populations. In some of the populations longer beaks may prevail, in others, shorter beaks may prevail, and in some populations the distribution may be roughly equal. This is due to the fact that the 'petty influences' (Galton's phrase) on each of the populations is different. As a result, the finches that are the fittest may not in fact have the greatest representation in the subsequent generation, due to the vagaries of disease, predators, lack of success in finding food, or simply being 'in the wrong place at the wrong time'. Now, it may be true that given *identical* conditions in each of the one hundred populations we would get exactly the same distribution in each population (although see Brandon & Carson, 1996 for an argument that natural selection is indeterministic; cf. Millstein, 2003), but it is hard to believe that this is what MDC have in mind given their concern to describe mechanism schemata (e.g., the operation of the Na⁺ channel) that can be instantiated in particular cases (e.g., the depolarization of a specific nerve cell). The bottom line is that natural selection is not regular in the way that MDC require (presumably because natural selection is not regular in the way the mechanisms that MDC discuss are, such as DNA transcription and protein synthesis).

This is not to deny that in the majority of the populations, the fitter finches (i.e., the finches whose beaks confer upon them a greater ability to obtain the most widely available seeds) will probably be more prevalent. Differently put, there is a certain degree of regularity to the outcomes of natural selection. Our point is just that this probabilistic regularity is a far cry from a mechanism that works always or for the most part in the same way under the same conditions. Comparing our discussion here of the probabilistic character of natural selection to our discussion of the issue in the context of Glennan's account (via Woodward), our understanding is that Glennan's account is more amenable to such probabilistic phenomena than MDC's is. If MDC allow for probabilistic mechanisms, they neither say so explicitly nor provide the tools with which to accommodate them.

To sum up, we have argued that natural selection is not organized in the ways Glennan or MDC argue, that productive continuity between its stages is not captured by either Glennan's 'interactions' or by MDC's 'entities' and 'activities', and that natural selection is not 'regular' in the way that MDC claim. We have also argued that natural selection is not captured by either of the broad types of mechanism Glennan distinguishes between, that is, systems-mechanisms and process-mechanisms. We are left with the conclusion that the new mechanistic philosophy, represented by its two dominant approaches, does not capture a main evolutionary mechanism. Because the results of the present section of the paper are negative, we conclude the paper in the next section with directions for further work in the new mechanistic philosophy. The aim is specific: we suggest directions

the new mechanists may take toward revising their conceptions of mechanism to capture natural selection.

5. Conclusion: directions for further work

This paper has been an exploration of the mechanism of natural selection under the rubric of the new mechanistic philosophy. We have shown that the main mechanism views, Glennan's (1996, 2002a,b) and MDC's (2000), fail to adequately characterize natural selection using our own schematized, mechanistic representation of it. Our analysis of natural selection on Glennan's and MDC's views delineated severe problems that cut across three key aspects of mechanisms, namely, organization, productive continuity, and regularity. In the brief discussion that follows, we sketch directions to take that may result in a conception of mechanism that captures natural selection and that may result in a more general conception of mechanism for the new mechanistic philosophy.

Consider the organization of mechanisms. Glennan and MDC have made strides in understanding tightly structured mechanisms. On Glennan's view, such mechanisms are complex systems decomposable into their component parts. His prime example is the toilet. On MDC's view, entities in mechanisms must be 'appropriately located, structured, and oriented', and their activities must have a 'temporal order, rate, and duration' (MDC, 2000, p. 3). MDC's prime examples are the mechanisms of protein synthesis and neuronal depolarization. At best, each of these apparently alternative ways of understanding the organization of natural selection is forced. At worst, neither of the alternatives make sense of the organization of natural selection. Natural selection is best understood as a non-unique causal chain of stages. As much structure or organization as is necessary for characterizing natural selection may be represented by capturing the dependencies between stages, represented in Figure 2. The idea of a non-unique causal chain of events accomplishes this. Given the resources provided by Glennan and MDC, two avenues for conceptualizing such a mechanism suggest themselves. First, one might revise Glennan's process-mechanism view so that such mechanisms may be *non-unique* causal chains of events rather than the *unique* chains he suggests. Second, one might relax the organizational strictures imposed on mechanisms by MDC in the relevant ways. We think the latter option might result in a more general conception of mechanism. After all, it would include both of Glennan's mechanism types under a univocal conception. However, greater generality with respect to organization may not be desirable if it means sacrificing an understanding of the things that make mechanisms distinctive in particular fields, such as molecular biology.

Considering productive continuity, we argued that neither Glennan's nor MDC's characterization is successful in the context of natural selection. Glennan's 'property change' conception of interaction is too narrow. The selective interaction, set out in stage (II) of Figure 1 above, is an interaction between organisms and their environment. However, the selective interaction is productive of change in survival and reproductive rates in the population (stages III and IV) by virtue of differences in

the ways in which organisms with certain forms of a trait exploit their environment given some critical factor within it. The move to MDC's entities and activities was not helpful. Providing a detailed account of organisms, the relevant entities, and their survival and reproduction activities provides an account of the different ways in which those organisms exploit their environments. However, as we saw, such a description does not provide an account of how the activities of those entities are productive of adaptive change. To capture natural selection as a mechanism, an account of productive continuity is required that captures the ways in which relevant property differences among a *population* of entities entering into causal interactions with their environment is productive of change in that population.

The third and final direction for further work we suggest concerns regularity. The regularity of mechanisms is not a problem unique to the new mechanistic philosophy. Rather, it is symptomatic of the more general problem of the nature and extent of applicability of scientific laws. MDC's conception of mechanism sidesteps this problem, suggesting that the regularity of mechanisms is exemplified by their working 'always or for the most part in the same way under the same conditions' (MDC, 2000, p. 3). We think MDC's reliance on such an informal understanding of regularity is problematic. Minimally, it appears not to be able to capture stochastic mechanisms such as natural selection. Or, at least, MDC's view seems better able to capture mechanisms that are not stochastic. MDC's informality with regard to regularity provides insufficient guidance for understanding mechanisms. We argued that Glennan's reliance on Woodward's (2000, 2003) conception of invariant generalizations to understand regularity is promising in relation to natural selection. That is, the extent to which Woodward's account of generalizations captures probabilistic mechanisms is the extent to which it holds promise for capturing natural selection. The upshot of our comments here is that the new mechanistic philosophy requires a clear exposition of causal relations in stochastic mechanisms. And while we think Woodward's work is promising, we further think that Glennan's (1997) distinction between stochastic/stochastic, deterministic/stochastic, etc. mechanisms is worth exploring in direct relation to a more general conception of mechanism.

In the context of natural selection, the most general statement we can make concerning directions for further work on the new mechanistic philosophy is this: to capture natural selection, a main evolutionary mechanism, a conception of stochastic mechanism as a non-unique causal chain is required in which change is produced by virtue of the ways in which property differences among members of a population in the context of some environment affect properties of that population. We think the basic resources for characterizing the mechanism of natural selection may be found in the new mechanistic philosophy. And we urge the proponents of the philosophy to explore the directions for further work we suggest.

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References

- Bechtel, W., & Richardson, R. (1993). *Discovering complexity: Decomposition and localization as strategies in scientific research*. Princeton, NJ: Princeton University Press.
- Brandon, R. (1980). A structural description of evolutionary theory. In P. D. Asquith, & R. N. Giere (Eds.), *PSA 1980, Vol. 2* (pp. 427–439) East Lansing, MI: Philosophy of Science Association.
- Brandon, R., & Carson, S. (1996). The indeterministic character of evolutionary theory: No 'No Hidden Variables Proof' but no room for determinism either. *Philosophy of Science*, 63, 315–337.
- Craver, C., & Darden, L. (2001). Discovering mechanisms in neurobiology. In P. Machamer, R. Grush, & P. McLaughlin (Eds.), *Theory and method in the neurosciences* (pp. 112–137). Pittsburgh: University of Pittsburgh Press.
- Darden, L., & Cain, J. (1989). Selection type theories. *Philosophy of Science*, 56, 106–129.
- Darden, L., & Craver, C. (2002). Strategies in the interfield discovery of the mechanism of protein synthesis. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 33C, 1–28.
- Dawkins, R. (1989). *The selfish gene*. New York: Oxford University Press.
- Futuyma, D. (1986). *Evolutionary biology* (2nd ed.). Sunderland, MA: Sinauer.
- Glennan, S. (1996). Mechanisms and the nature of causation. *Erkenntnis*, 44, 49–71.
- Glennan, S. (1997). Probable causes and the distinction between subjective and objective chance. *Noûs*, 31, 496–519.
- Glennan, S. (2002a). Contextual unanimity and the units of selection. *Philosophy of Science*, 69, 118–137.
- Glennan, S. (2002b). Rethinking mechanistic explanation. *Philosophy of Science*, 69(Suppl.), S342–S353.
- Grant, B. R., & Grant, P. (1989). *Evolutionary dynamics of a natural population: The large cactus finch of the Galapagos*. Chicago: University of Chicago Press.
- Hartl, D., & Clark, A. (1989). *Theoretical population genetics*. Sunderland, MA: Sinauer.
- Hull, D. (1988). *Science as a process: An evolutionary account of the social and conceptual development of science*. Chicago: University of Chicago Press.
- Hull, D., Langman, R., & Glenn, R. (2001). A general analysis of selection. *Behavioral and Brain Sciences*, 56, 511–573.
- Kitcher, P. (1989). Explanatory unification and the causal structure of the world. In P. Kitcher, & W. Salmon (Eds.), *Scientific explanation*. (pp. 410–505). Minnesota Studies in the Philosophy of Science, XIII. Minneapolis: University of Minnesota Press.
- Lennox, J., & Wilson, B. (1994). Natural selection and the struggle for existence. *Studies in History and Philosophy of Science*, 25, 65–80.
- Lewontin, R. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Machamer, P., Darden, L., & Craver, C. (2000). Thinking about mechanisms. *Philosophy of Science*, 67, 1–25.
- Millstein, R. (2002). Are random drift and natural selection conceptually distinct? *Biology and Philosophy*, 17, 33–53.
- Millstein, R. (2003). How not to argue for the indeterminism of evolution: A look at two recent attempts to settle the issue. In A. Hüttermann (Ed.), *Determinism in physics and biology* (pp. 91–107). Paderborn, Germany: Mentis.

- Millstein, R. (unpublished). Populations, probability, and natural selection. Presented at the biennial meeting of the International Society for the History, Philosophy, and Social Studies of Biology, Vienna, Austria, July 2003.
- Roughgarden, J. (1996). *Theory of population genetics and evolutionary ecology: An introduction*. Englewood Cliffs, NJ: Prentice Hall.
- Rudge, D. W. (1999). Taking the peppered moth with a grain of salt. *Biology and Philosophy*, 14, 9–37.
- Salmon, W. (1998). *Causality and explanation*. New York: Oxford University Press.
- Skipper, R. (1999). Selection and the extent of explanatory unification. *Philosophy of Science*, 66(Suppl.), S196–S209.
- Skipper, R. (2001). The causal crux of selection. *Behavioral and Brain Sciences*, 24, 556.
- Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. Chicago: University of Chicago Press.
- Woodward, J. (2000). Explanation and invariance in the special sciences. *British Journal for the Philosophy of Science*, 51, 197–254.
- Woodward, J. (2002). What is a mechanism? A counterfactual account. *Philosophy of Science*, 69(Suppl.), S366–S377.
- Woodward, J. (2003). *Making things happen: A theory of causal explanation*. New York: Oxford University Press.