Defusing Ideological Defenses in Biology

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Ideological language is widespread in theoretical biology. Evolutionary game theory has been defended as a worldview and a leap of faith, and sexual selection theory has been criticized for what it posits as basic to biological nature. Views such as these encourage the impression of ideological rifts in the field. I advocate an alternative interpretation, whereby many disagreements between different camps of biologists merely reflect methodological differences. This interpretation provides a more accurate and more optimistic account of the state of play in the field of biology. It also helps account for biologists' tendency to embrace ideological positions.

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Defenders and critics of one or another approach in theoretical biology sometimes employ sweeping, ideologically loaded claims in support of their positions. By this, I mean that differences in viewpoint or methodology are construed as resulting from incompatible research programs, each committed to a different view of biological reality. I witnessed one possible result of such a construal a few years ago, when two biologists with different research programs, addressing different types of phenomena, each volunteered an opinion of the other's work. In the view of biologist A, biologist B was "no longer doing biology." Biologist B independently offered the opinion that biologist A was "not a colleague" of hers. Although this was an extreme example of divisiveness, I have witnessed similar exchanges in other groups of biologists, both in print and over dinner. (I do not suggest that such scenarios are more common in biology than in other disciplines; the situation in theoretical biology is simply my focus in this article.) Yet these same biologists collaborate in a variety of ways. For instance, biologists A and B have coauthored publications and shared students. To my mind, this suggests that the presentation of such differences as commitments to fundamentally opposed views of biological reality is ripe for reconsideration. Let us begin by considering two examples of disagreements that have been construed as ideological.

The optimization research program

Gould and Lewontin (1979) ushered in an era of polarization in evolutionary biology between "adaptationists" and their critics. In their highly influential paper, Gould and Lewontin explicitly cast as ideology the approach of proposing an adaptive explanation for traits considered individually. They coined an *-ism* for this approach, and they employed religious metaphors to characterize the view. Thus *adaptationism* "is based on faith in the power of natural selection" and employs the "catechism" that genetic drift is a significant influence only in unusual, unimportant circumstances. The adaptationist refuses to credit other causes such as drift with any real influence while "[congratulating him- or herself] for being such an undogmatic and ecumenical chap." This construal saddles a type of methodology in evolutionary biology with ideological baggage and then criticizes it as false dogma.

Optimization models, including evolutionary game theory, employthe procedure that Gould and Lewontin (1979) drew into question and are therefore one of the primary targets of their criticisms. Many biologists do not accept Gould and Lewontin's (1979) ideological gloss of optimization modeling; they instead subscribe to Maynard Smith's (1982) interpretation of the point as simply the methodological corrective that optimization models should reflect constraints arising from evolutionary influences other than natural selection. However, a number of defenses of the optimization approach—and of evolutionary game theory in particular—have embraced the construal of their position as ideological. Grafen (1984) coined the term *phenotypic gambit* to describe commitment to the optimization approach, which he acknowledged is a "leap of faith." Mitchell and Valone (1990) endorsed what they called the *Optimization Research Program*, citing Lakatos's view of research programs, the core hypotheses of which adherents should protect from disconfirmation at all costs. Brown (2001) accepted this construal and defended the Optimization Research Program as his "worldview," with game theory at its center. A prominent style of defending optimization modeling thus qualifies as ideological in the sense identified above. It is expressed as a commitment to a particular view of biological reality, a commitment that is taken to preclude other approaches.

Criticisms of sexual selection theory

Sexual selection theory is a well-developed set of hypotheses for the role of selection in the

evolution of a variety of sexual and reproductive traits. Different versions of the theory vary in important respects, but I will attempt to give a basic summary that applies to most versions. In many animal species, males (and perhaps sometimes females) are expected to differ in their mating success, which creates selection pressure for traits desirable to members of the opposite sex or useful in competing with others of the same sex. Thus, the peacock's long, colorful train is explained as the result of peahens preferentially mating with comely-trained peacocks, not by any survival advantage conferred by the trains. Similarly, the evolution of combat among male bighorn sheep is explained as the result of ewes preferentially mating with the victors. Traits classically explained as the result of sexual selection range from physical traits, such as ornamentation, to behavioral traits, such as combat displays or parental care. The basic tenets of sexual selection theory are widely accepted in biology, though as I mentioned above, there are disagreements about various features of the theory, and the hypotheses have been updated and fine-tuned to accommodate ever-expanding information about animals' bodies and behavior (e.g., Clutton-Brock 2009).

However, the past decades have also seen a number of criticisms of sexual selection theory. Here I will focus on recent criticisms put forth by Roughgarden (2009; see also Roughgarden 2004, Roughgarden et al. 2006). Roughgarden analyzed and thoroughly rebutted a wide range of hypotheses about the evolution of sex, gender, and reproductive behavior that she attributed to sexual selection theory. Toward the end of the book, Roughgarden argued that she had shown that all those hypotheses are false, that there is no reason to amend the hypotheses, but that sexual selection theory is "a philosophy of biological nature" with an "incorrect foundation" (2009, p. 246). In Roughgarden's view, the hypotheses all "derive from a common view of natural behavior predicated on selfishness, deception, and genetic weeding" (2009, p. 247). Roughgarden suggested that, instead, kindness and cooperation are "basic to biological nature" (2009, p. 1). She thus proposed an alternative *social selection theory*, based on the contrary assumptions of "teamwork, honesty, and genetic equality" (2009, p. 247). Roughgarden, then, construed her disagreement with sexual selection theorists as fundamental and thoroughgoing, based on opposed beliefs about what is biologically basic. She represented the options as complete commitment to or else complete rejection of all the hypotheses that she identified with sexual selection theory.

In both of these debates, the options are presented as sweeping commitments to positions that are polar opposites. Either you subscribe to the Optimization Research Program as your

worldview, or you reject it. Either you jettison all of sexual selection theory, or else you commit to the sexual-selectionist view of the basics of biological nature. These positions are presented as ideological in the sense that they involve adherence to a systematic set of ideas, a comprehensive way of looking at things. The set of ideas in question is viewed as fundamental to the domain under investigation, and adherence to one side or the other is taken to be a total commitment. This ideological tenor thus suggests that there is a rift in theory, that there is dispute regarding the basic understanding of these types of phenomena. Here I develop an alternative interpretation, according to which these disagreements and others like them are more fruitfully seen as rooted in methodological, not ideological, differences. This methodological interpretation provides a more accurate account of how the field of biology functions and a more optimistic take on the state of play in the field. It also suggests a rationale for why some theoretical biologists embrace polarized, ideological positions.

Before proceeding, a couple of clarifications are in order. First, by claiming that these positions are presented as ideological, I do not mean to suggest that they are necessarily influenced by broader social ideology. Other research demonstrates that this is frequently the case; Richardson (1984), for instance, developed this point for both of my present examples. Yet the focus of this article is not the influence of broader social values on theoretical biology, but the construal of debates as ideological in the particular sense identified above. Second, although I will argue that many debates in biology presented as ideological are more fruitfully understood as methodological debates, this may not hold true for all such debates. There is certainly room for disagreements in theoretical biology that really do involve commitments to fundamentally opposed positions. One goal of the present analysis is therefore to provide resources for distinguishing methodological differences from truly opposed "worldviews."

Distinguishing idealizations from ideology

There is room for an alternative interpretation of debates in theoretical biology like the two surveyed above, despite their ideological tenor. The starting point is philosophical treatments of the role of modeling in science. The scientific practices that have been termed *model-based science* account for the persistence of multiple modeling approaches (e.g., Levins 1966, Godfrey-Smith 2006, Weisberg 2006). According tothis view, idealized models represent targeted features of a system at the expense of misrepresenting other features. Different modeling approaches

thuscan seem to be incompatible, for they employ different parameters and opposed assumptions, when instead the exact opposite is true. The limitations of idealized models make the use of multiple approaches essential. Taking to heart the idea that models provide a limited representation of only targeted features of a phenomenon makes clear that no single modeling approach offers an exhaustive, fully accurate account of any phenomenon.

This view of model-based science enables an interpretation of seemingly ideological debates in biology as instead methodological at root. (I use the concept *methodology* broadly, to include modeling approaches and their accompanying assumptions.) Despite the rhetoric that is sometimes employed, the question to ask about apparently competing modeling approaches is often not which is grounded on a more successful worldview, but which method better serves one's present research aims. Several aspects of this shift are important. On the methodological interpretation, proposed modeling approaches should be evaluated not according to universal ontological considerations—what the world is posited to be like overall—but according to considerations of method, especially representational capacity. The evaluation is thus not an absolute judgment, but is contingent on the aims of representation for the research program at hand. This means that different methods may very well be called for in different circumstances, and so a variety of approaches may be warranted. The key features of this interpretation of a debate are therefore :(1)the resolution depends on an evaluation of methodology; (2) the choice of approach is contingent on the present research aims: and (3) multiple approaches can coexist without difficulty. These distinguishing characteristics of ideological and methodological disagreements are represented in table 1.

Table 1: The distinguishing features of ideological and methodological disagreements.

Feature	**Ideological difference**	**Methodological difference**
Basis of evaluation	What the world is like	Method, representational aims
Scope of position	Complete "worldview"	Contingent on research program
Commitment to approach	Absolute; either–or	Multiple approaches can coexist

Some disagreements in biology are patently methodological, but many admit of both construals, including disagreements traditionally interpreted as ideological. This is so for the two debates on which I focus in this article, as I will demonstrate below. There are also some debates

for which an ideological construal will remain appropriate. To consider an extreme example, embracing basic evolutionary theory commits one to a systematic set of ideas about a type of process and its range of possible results. This set of ideas is fundamentally opposed to "intelligent design." There is not room for both;arguments for intelligent design presume the impossibility of large-scale evolution. Intelligent design therefore cannot be defended solely on the basis of its representational aims.

Let us now reexamine the previously discussed debates, to the end of showing that in both cases a methodological interpretation is not only possible but also preferable. Although several defenses of the optimization approach have construed the approach as a commitment to a worldview, or a matter of faith, another construal is available. Maynard Smith (1982), for one, attempted to refocus the debate on methodology. This is as strong of a defense as is needed to justify the modeling approaches of optimization and evolutionary game theory, and it is a more defensible position than an ideological defense. Too much research has been devoted to nonselective causal influences, such as available genetic variation and developmental pathways, for most biologists to subscribe to the notion that selection is the only evolutionary influence. To say that selection is often the only *important* influence, as some have done, is just to declare a preference for tracking that causal process over others. It is more straightforward and more promising to instead defend optimization as simply one modeling approach among many in biology, each with a specific representational focus and delimited range of application.

Mitchell and Valone (1990) represent the debate over the use of game theory as a choice between embracing either the assumptions of evolutionary game theory or those of quantitative genetics, but this is wrong. Certain assumptions of each of these modeling approaches are undeniably idealized, and there are just as obvious limitations to each approach's range of applicability to evolutionary phenomena (Potochnik 2010). These considerations indicate that game theory and quantitative genetics are each motivated by specific and limited representational goals. Each facilitates the faithful representation of some features of some types of evolutionary scenarios. It follows that neither set of assumptions is sufficient for all projects in population biology, which is why both approaches persist. The methodological defense thus better accounts for game theory's role in population biology than does the ideological defense.

The ideological tenor of Roughgarden's (2009) criticisms of sexual selection theory played an important role for her argument. Advocating the rejection of sexual selection theory in

its entirety draws attention to assumptions shared by many of the theory's specific hypotheses, such as competition for mating opportunities and the default traits of each sex, and the regards in which those assumptions may be problematic. However, a methodological version of Roughgarden's (2009) criticisms could still accomplish this. This alternative, methodological approach would be to point out the range of phenomena treated by sexual selection models and the assumptions or idealizations that the models share. This would set up the desired contrast with Roughgarden's (2009) social selection theory, which encompasses a different range of phenomena and employs different assumptions. For instance, whereas sexual selection theory addresses scenarios in which same-sex animals compete for mating opportunities, social selection theory addresses scenarios in which the outcomes or selection effects are mediated by social interactions. These groupings of evolutionary phenomena overlap partially but not entirely. Further, whereas sexual selection theory assumes that direct competition among same-sex individuals is the norm, social selection theory assumes that a mutually beneficial outcome is within evolutionary reach. It is possible—even likely—that each assumption is right some of the time. Roughgarden and sexual selection theorists would probably disagree about the frequency with which each assumption obtains, but this revised disagreement is methodological in nature.

An advantage of this methodological version of Roughgarden's (2009) criticisms is that it would provide a less polarizing introduction to the many distinct positive views that she advocated, including the alternative modeling techniques that she suggested (Potochnik 2012). Roughgarden (2009) lumped her suggestions for modeling approaches together with her complete rejection of sexual selection theory and controversial alternative hypotheses. Faced only with the choice of wholesale rejection or acceptance of those views, many reject them. (Consider, for instance, the critical letters written by over fifty individuals in response to Roughgarden's related article in *Science* [Roughgarden et al. 2006, Kavenagh 2006]). But this need not be so. Roughgarden's (2009) suggestions for modeling behavioral evolution, which emphasized malleable selection effects due to influences such as negotiation and punishment, are distinct from her specific hypotheses for the evolution of traits related to sex, gender, and reproduction. A methodological approach at once facilitates Roughgarden's (2009) criticisms of background assumptions shared by many sexual selection hypotheses and also renders her various ideas separable and thus potentially palatable to a broader group of biologists.

These examples of disagreements in theoretical biology can therefore be profitably

interpreted as rooted in methodological differences, despite the tendency of several biologists to construe the differences as ideological in nature. The same is true of other debates in biology that are similarly structured, such as the long-standing disagreements surrounding group selection and, perhaps, the significance of developmental processes for evolutionary outcomes. Recall that I do not expect *all* apparently ideological debates to be resolved on methodological grounds. Instead, each debate must be examined to see whether it can be profitably construed as possessing the features of a methodological disagreement, as summarized in table 1. On the methodological interpretation, competing approaches should not be evaluated according to which is true or the basis of a successful worldview, and a total commitment to an approach is unwarranted. The evaluation is instead based on which types of systems and which features of those systems are central to one's present research program and which approach best meets those representational aims.

Notice that, even when a methodological interpretation is appropriate, there may still be disagreements about matters of fact. For instance, two biologists may well disagree on whether natural selection is a significant causal factor in the evolution of a particular trait. But such disagreements need not amount to universal commitments, and they are not the only reason for variation among biologists' methods. The methodological interpretation of disagreements in theoretical biology keeps models' aims and limitations at center stage, which results in the evaluation of an approach contingent on the aims of research and the likelihood of the coexistence of multiple approaches in a stable area of research.

Normal science with a twist

Features of this methodological interpretation of debates can actually help account for why some biologists on each side of divisive issues embrace polarized, ideological positions. I have suggested that research programs within biology differ in ways that warrant employing certain modeling approaches to the exclusion of others. For both central and accidental reasons, participants in different research programs focus on different phenomena, are acquainted with different bodies of past research, and even may have familiarity with different varieties of organisms. This means that advocates and critics of a modeling approach address that approach from different perspectives, for they often differ in both interests and expertise. Such differences can easily lead to disagreements about the commonness of types of phenomena and the

significance of causal patterns. Those engaged in optimization research are quite familiar with the successes of optimal foraging theory, and they dismiss the overdominance of malaria resistance as an uncommon if not unique genetic situation. Similarly, Roughgarden's (2009) hypotheses led her to focus on animal species with extensive social interactions, such as shared care of young or collective hunting.

Another ingredient of ideological stances in theoretical biology is an implicit commitment to the existence of simple causal processes with broad domains of application. A tacit belief in such magic-bullet causes enables differences in focus and expertise among researchers to be interpreted as commitments to different types of causes. If it is instead agreed that most phenomena are influenced by a vast array of causal factors, then researchers' differences are naturally understood to arise from a difference in focus, not a difference in worldview. In this case, the claim that certain features of the evolutionary process are more important is reduced to the claim that some are worthier of investigation than others. Put this way, it is not an empirical claim, but merely a statement of research interests (see Godfrey-Smith [2001] on this point regarding adaptationism in particular).

This account of how ideological positions in theoretical biology arise in a sense explains away such ideological tendencies. However, I should emphasize that the posited account attributes more significance to ideological positions than, say, the idea that these stances are simply adopted as a way to increase recognition or funding. In my view, standoffs between opposed ideological positions indicate something important about the field of biology. That there are such entrenched proponents and opponents of different methods indicates that a variety of modeling approaches have some purchase on the evolutionary process and other biological phenomena. In my view, this reflects the complex causal processes at work in biological phenomena and the endless variety of how causal factors combine and interact. There are evolved traits such as foraging behavior that optimization analysis readily predicts; those such as sickled red blood cells with which it can get nowhere; and a whole range of intermediate traits for which it is partially successful insofar as it represents the causal contribution of natural selection, which may be just one causal influence among many. The causal influences on the physical characteristics and social behavior of animals are likely to be as diverse as those traits themselves, so there is room for sexual selection theory's success with some and its failure with others.

Recasting ideological differences as methodological differences also grounds a more

optimistic interpretation of the current state of play in theoretical biology. The diversity of approaches does not stem from a clash of worldviews, and so biology is not in a state of crisis from which one research program will emerge triumphant. Instead, strong ideological differences persist within a functional field of research. This will continue to be the case as long as different methodologies are useful for different research programs.

So, then, why does the main point of this article matter? If ideological differences are consistent with a fully functional field of science, why concern oneself with the reinterpretation that I suggest? In my view, were more biologists and philosophers of biology to embrace this interpretation of commitment to favored modeling approaches, real, advantageous consequences would result. Most basically, less attention would be devoted to arguments that are, as it turns out, simply about focal phenomena and modeling approaches of choice. A prime example is the decades of continuing debate in philosophy of biology over adaptationism, when optimization approaches can instead be motivated on much more modest grounds (Potochnik 2009).

Adopting the methodological interpretation would also promote cooperation among those who continue to have substantive disagreements about biology. Instead of becoming mired in ideological impasse, focusing on modeling approaches allows communication and progress in spite of different views about how the models apply to the real world. As Godfrey-Smith (2006) put the point,

> When much day-to-day discussion is about model systems, disagreement about the nature of a target system is less able to impede communication. The model acts as a buffer, enabling communication and cooperative work across scientists who have different commitments about the target system (p. 739).

According ton this view, continuing disagreements about evolutionary phenomena need not hinder cooperative work on the features of models. If all parties can—at least temporarily—set aside differences in commitment to broad claims of causal importance, they can further joint understanding of models' inner workings and the conditions for their application. Indeed, I have observed this firsthand at meetings of a working group on evolutionary game theory (at the National Institute for Mathematical and Biological Synthesis).

Finally, the refocus facilitated by a shift to the methodological interpretation of disputes

creates more room for activities of significance for theoretical biology and the philosophical analysis of biology. Recognition of the viability of a range of modeling approaches and the related idea of complex and variable causal processes should lead to a diminished focus on isolated, illustrative applications of a type of model. This should be replaced by an increased focus on determining the range of and conditions for a modeling approach's applicability and the limitations of its assumptions, as well as increased attention to the interplay among multiple causal influences. For philosophers of biology, the lesson is to expect a continual plurality of methods in biology—methods that can appear contradictory—and to take with a grain of salt any claim that one or another approach is the key to understanding biology.

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