

In short, Roughgarden is vindicated in offering a revolutionary alternative to sexual selection and not a mere revision to existing views. And Darwin is vindicated in his separation of natural selection from sexual selection.⁵

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The primary purpose of *The Genial Gene* is to criticize the many individual hypotheses grouped under the rubric of sexual selection theory and to develop alternative hypotheses that account for the traits in question. Roughgarden identifies 26 empirical hypotheses, on issues ranging from the evolution of sexual reproduction and sexual dimorphism to the behavioral ecology of mating, reproduction, and the rearing of young (237–238). Together, these comprise the empirical content of social selection theory.

Yet, the empirical hypotheses are not the entirety of the project. Roughgarden's first sentence declares that "this book is about whether selfishness and individuality, rather than kindness and cooperation, are basic to biological nature" (1). My aim here is to establish the role that this claim plays in Roughgarden's research program. The broad-scope theoretical claim that cooperation is basic plays a fundamental and intriguing role in Roughgarden's project. Understanding that role uncovers an important element of Roughgarden's criticism of sexual selection theory. It also is key to understanding the nature of Roughgarden's dissatisfaction with other accounts of the evolution of cooperation.

Debunking selfishness

Roughgarden's claim that kindness and cooperation are basic to biological nature is more than an opening line; it plays an important role in her project. What to make of that role is part of what is at issue between Roughgarden and sexual selection theorists. It is also a non-trivial part of understanding social selection theory. In this section, I critically examine how Roughgarden's ideas about the basics of biological nature contribute to her research program.

Near the end of the book, there is a brief argument for the rejection of sexual selection theory in its entirety. Roughgarden asks the reader to "consider the implications of sexual selection being incorrect on all 26 [empirical hypotheses]" (247). She argues that, if the sexual selection hypotheses were mutually independent, the chances that they *all* would be wrong are vanishingly small. She concludes that, instead,

some feature common to all 26 propositions in sexual selection must exist to explain why they are all incorrect at the same time. That feature is that all 26 points derive from a common view of natural behavior predicated on selfishness, deception, and genetic weeding. If this view of biological nature is

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wrong, then deriving any 27th or 28th additional element for [the sexual selection system] will fail as well. Thus, the sexual selection system cannot be somehow repaired or sanitized. Its foundation is incorrect (247).

Roughgarden claims that sexual selection theory is a codification of the view that selfishness etc. characterizes the evolved traits related to gender, sex, and reproduction. In this passage, she suggests both that the view that selfishness is basic influences the nature of sexual selection hypotheses and that the incorrectness of those hypotheses indicates that the belief that selfishness is basic is false.

Let us consider these two ideas individually. According to the first, a view about what is biologically basic influences the empirical hypotheses that are generated. It is clear that broad-scope beliefs play this role for Roughgarden's social selection theory—namely, the belief that kindness and cooperation are commonplace in the living world. For example, Roughgarden (2004) initially conceded that the peacock's colorful train fits within the sexual selection framework. Takahashi et al.'s (2008) empirical findings against the role of this train in mate selection led Roughgarden to reconsider. Her view that cooperation is commonplace in the animal kingdom then sparked the hypothesis that the peacock's train fits into that rubric: perhaps social dynamics, not sexual dynamics, give a colorful train its value. Empirical findings against the female mate-choice hypothesis occasioned this new hypothesis, and empirical findings will decide the success of Roughgarden's replacement hypothesis. But the formulation of the new hypothesis was surely influenced by antecedent views about the character of the living world.

In Roughgarden's view, sexual selection theory is similarly guided by a commitment to selfishness. If so, that commitment is generally left unarticulated by sexual selection advocates. Yet, broad-scope beliefs of some sort do play a role in sexual selection theory. In response to challenges to some sexual selection hypotheses, Clutton-Brock (2007) responds that "the theory of sexual selection still provides a robust framework that explains much of the variation in the development of secondary sexual characters in males." One role of sexual selection theory is as a framework that guides the formulation of individual empirical hypotheses, much as an explicit commitment to cooperation guides Roughgarden's hypotheses.

Yet, Roughgarden risks overstating the connection between background views and empirical hypotheses. A view of what is basic to biological nature cannot issue direct predictions about the living world. Even if kindness and cooperation are basic, there is a great deal of latitude in how kindness/cooperation is manifested, as Roughgarden (2004) amply demonstrates. Additionally, views of what is basic to biological nature not only accommodate a variety of manifestations in the living world but also allow occasional departures from the pattern. Roughgarden allows that some behaviors may be best described in terms of conflict, and Clutton-Brock (2007) allows for instances of mating behavior that do not conform to the pattern of female choice. A view about what is basic can inspire empirical hypotheses, but it certainly does not entail them.

The second relationship that Roughgarden posits between the view that selfishness is basic and sexual selection theory runs in the opposite direction. She claims that demonstrating that the empirical hypotheses of sexual selection are

incorrect *falsifies* the view that selfishness is basic to biological nature. Surely, this is wrong. Even assuming that the empirical hypotheses in question are motivated by the view that sexual behavior is based on “selfishness, deception and genetic weeding,” the failure of those hypotheses does not wholly undermine this view of biological nature. I have argued that a claim about what is biologically basic does not prescribe particular empirical hypotheses but is consistent with a variety of hypotheses. Accordingly, the failure of any number of empirical hypotheses cannot falsify a view of the basics.

Disconfirmation of any sort seems the wrong way to think about the relationship between empirical claims and broad-scope claims about what is basic. If the latter does not issue specific predictions, then it is not directly subject to confirmation or refutation. A view of what is basic to biological nature is better seen as a guiding heuristic, judged according to its fruitfulness rather than its truth. The connection between empirical observations and a claim that, e.g., selfishness is biologically basic is heavily attenuated. Selfishness may be defined in any number of ways for a wide variety of phenomena. It is also unclear what range of influence to expect from a quality dubbed basic. The scientific value of a view about what is biologically basic is its ability to inspire novel empirical claims, claims that *can* be confirmed or disconfirmed.

This idea is supported by points made above. A view of what is basic to biological nature is compatible with any specific empirical outcomes, indeed, can engender an array of distinct hypotheses for a single phenomenon. Consider also the relationship among empirical hypotheses inspired by some view of the basics. Only for closely related phenomena can the accuracy of a hypothesis for one phenomenon provide evidence of its accuracy for another. For instance, if a rich cooperative social network is discovered in one species of birds, this is some evidence for similar networks in other species. Expectations for similar dynamics in substantively similar evolutionary outcomes are based on more than broad claims about what is basic to nature. In contrast, the success of hypotheses for more disparate phenomena is virtually independent. The cooperative rearing of young in birds gives no evidence that anisogamy (the egg/sperm binary) evolved for mutual advantage, even if both hypotheses result from the view that cooperation is basic to biological nature.

Sexual selection hypotheses about the evolution of sex, gender, and reproduction succeed or fail individually, as relatively independent claims about evolution. The same is true for Roughgarden’s competing empirical hypotheses. A commitment to the view that kindness and cooperation are basic does not warrant accepting those hypotheses, nor does the rejection of that view warrant rejecting those hypotheses. Some evolutionary outcomes are best described in terms of conflict (203), but this alone does not undermine the claim that cooperation is “basic.” Similarly, the success of social selection theory would not falsify, or even disconfirm, the idea that selfishness is basic. Empirical claims about the world do not proceed in lockstep with a view of what is basic.

However, a view of what is biologically basic is not entirely beyond the purview of empirical results. If, as I suggested, a view of the basics should be judged for its fruitfulness, then an unfruitful view of the basics should be jettisoned. The debate

over social selection theory includes a disagreement on precisely this point. Each side accuses the other of imposing a favored worldview that is not reflected in the living world. Coyne (2004), in a review of Roughgarden (2004), claims that “[Roughgarden’s] agenda... is explicit and ideological.” Roughgarden responds in kind. She says, “Neo-Spencerists have not scientifically demonstrated their world view of nature. They have merely stipulated it and ridicule any alternative view of nature as romantic wishful thinking” (3). Each posits that one view of what is biologically basic generates plausible empirical hypotheses about gender, sex, and reproduction and that the competing view is imposed as an interpretation—a *misinterpretation*—of those traits. This can be viewed as a disagreement over the fruitfulness of different views of the basics.

In summary, Roughgarden’s insistence that her book is about what is “basic to biological nature” is not empty rhetoric. Her criticisms of sexual selection theory are partly inspired by her commitment to the roles of kindness and cooperation, and the points of dispute include the role played by competing broad-scope commitments. Roughgarden’s work exemplifies the socially engaged science proposed by Longino (1990). Yet, Roughgarden’s claim that she has falsified the view that selfishness is basic is incorrect. Instead, the success of her criticisms should be judged by whether she has demonstrated that selfishness and deceit are common evolutionary hypotheses not because they are commonplace in the living world, but because of a misguided theoretical commitment. Roughgarden should not aim to falsify a commitment to selfishness but to demonstrate its unfruitfulness.

Accounting for cooperation

Roughgarden distances her approach from other attempts to account for cooperation in nature. She is critical of accounts of the evolution of altruism in terms of group selection, reciprocal altruism, or kin selection. Given her emphasis on cooperation, it is initially a bit mystifying why Roughgarden regards these models for the emergence of cooperative behavior as foes instead of friends. Here too, her broad-scope claim that cooperation is basic is at the heart of her criticisms.

Roughgarden’s primary criticism of kin selection and reciprocal altruism is that both “are theories whose purpose... is to take the altruism out of altruism—theories that devise a way to see how cooperative behavior is really deep-down selfishness after all” (3). These theories account for cooperation by showing how cooperative behavior leads to advantage at the level of genetic inclusive fitness (kin selection) or as a product of repeated interactions (reciprocal altruism). An advocate of the “selfish gene” view may construe this as selective advantage as the product of selfishness, either at the genetic or at the individual level (12). This makes cooperation illusory, thereby violating Roughgarden’s commitment to cooperation as basic.

Roughgarden’s contention against group selection is that, though theoretically possible, the differential success of groups is not common. Behavior, even social behavior, leads to fitness consequences for individuals (12). Roughgarden’s concern seems to be that group-selection models assume that individual-level selection acts

against cooperative behavior and is counteracted only by group-level selection for cooperation. Again, cooperation is taken to be non-basic. In contrast, Roughgarden expects that “ordinary individual-level natural selection” often favors cooperation (186). No special appeal to a different level of advantage is needed; cooperation simply pays off.

Here, Roughgarden’s criticisms of approaches to accounting for cooperation converge. Roughgarden notes that kin selection models and group-selection models are mathematically equivalent (e.g., Kerr and Godfrey-Smith 2002) and that both represent selection acting in opposed directions. Group-selection models represent individual-level selection against cooperation and group-level selection for cooperation. Kin selection models incorporate into a gene’s inclusive fitness the fitness cost to gene copies in benefactors and the fitness benefit to gene copies in beneficiaries. Both assume cooperation has a cost. In contrast, Roughgarden’s commitment to cooperation as basic leads to the expectation that cooperation often results in direct selective advantage (185–186).

In the levels of selection debate, altruistic behavior is commonly defined as behavior that benefits others at a personal fitness cost (Sober and Wilson 1998). This suggests that any behavior that benefits the actor is selfish, a definition that Roughgarden criticizes. Choosing this dividing line between selfishness and altruism makes selfishness the evolutionary default: any behavior that results in individual selective advantage is, by definition, selfish. Any account of the evolution of cooperation that employs this definition of selfishness—including kin selection, reciprocal altruism, and group selection—prejudges the question of what is basic to biological nature.

Roughgarden suggests an alternate definition of cooperation that does not equate direct fitness advantage with selfishness. She argues that models of social behavior should explicitly represent both (1) how behavior develops during the life span of individuals and (2) how behavioral strategies evolve through evolutionary time. Then, cooperation can be defined in terms of behavioral dynamics, rather than simply selection dynamics. As Roughgarden et al. put the point,

The distinction between our proposition and previous work is apparent in the use of the word cooperative, which means only a mutually beneficial outcome in previous work but describes a process of perceiving and playing the game in our work (2006, 967).

Defined in terms of behavioral dynamics, cooperation need not involve a cost to direct fitness. Instead, cooperation is defined by how social interactions are approached. For example,

through reciprocal calls and physical intimacy, players perceive team fitness and act accordingly rather than play solely as individuals. Communication during courtship permits bargaining and promises of side payments (2006, 966–967).

In this scenario, individuals have recourse to bargaining, side payments, and threat points to ensure mutually advantageous arrangements. Yet, the arrangement

qualifies as cooperative, for social behavior is employed to accomplish mutual advantage.

In Roughgarden's view, other approaches err in the assumption that cooperation cannot be directly advantageous. Those approaches assume either that cooperation comes about through a separate form of selective advantage (group fitness or inclusive fitness) or that cooperation is at root selfishness (reciprocal altruism). In contrast, Roughgarden claims that "many instances of cooperative behavior are best explained as the kind of team play envisioned in our behavioral tier, combined with ordinary individual-level natural selection in the evolutionary tier" (186). She thinks that once cooperation is adequately defined, it is not an evolutionary enigma, but a common successful strategy.

This is another role played by the commitment to kindness and cooperation as basic. Eliminating the assumption that individual advantage simply *is* selfishness creates room for the hypothesis that cooperation emerges via individual selective advantage. Yet, this brings to the fore another difficulty with how Roughgarden wields her broad-scope theoretical claims. Notice that Roughgarden's preferred definition of cooperation applies only to social behavior, to organisms that have the potential to engage in team play. This is not relevant to some traits Roughgarden deems cooperative. For instance, she postulates that anisogamy is due to mutual advantage rather than sexual conflict. But if the physical trait of gamete size is to count as a cooperative outcome, the definition of cooperation must be altered to include non-behavioral traits. The behavioral sense of cooperation is not broad enough to be basic to biological nature.

This illustrates how different conceptions of the basics may lead to an overemphasis of differences. Roughgarden's criticism that group selection and kin selection are not common evolutionary mechanisms is an empirical disagreement with advocates of those views. In contrast, her criticism that group selection, kin selection, and reciprocal altruism consider all individually advantageous behavior to be selfish is a dispute about words rather than the world—it hinges on the definition of "selfishness". Roughgarden's criticism on this point does not preclude the possibility of, e.g., successful reciprocal altruism models. It simply allows for disagreement over whether the behavior in question should be considered selfish.

If Roughgarden is right that flawed evolutionary explanations result from the assumption of widespread selfishness, perhaps the proper lesson is not to assume widespread cooperation, but to avoid committing to *any* view of what is basic to biological nature. The success of Roughgarden's empirical hypotheses will likely vary from case to case; as Roughgarden readily acknowledges, much empirical work remains. The extent of empirical differences is also yet to be determined. The danger of any wholesale commitment to what is basic to nature is that it may obscure failures of the favored theory and empirical equivalences with other theories. Perhaps the true value of the claim that cooperation is basic is in its power to undermine implicit assumptions of the opposite.⁶

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