INTRODUCTION Is Nature Selfish?

This book is about whether selfishness and individuality, rather than kindness and cooperation, are basic to biological nature. Darwinism has come to be identified with selfishness and individuality. I criticize this evolutionary perspective by showing it misrepresents the facts of life as we now know them. I focus on social behavior related to sex, gender, and family where the reality of universal selfishness and sexual conflict is supposedly most evident. I show that writings in the professional biological literature advocating a picture of universal selfishness, as well as similar writings in books and articles aimed at the general public, are mistaken. I present my laboratory's alternative evolutionary theories for social behavior that emphasize cooperation and teamwork and that rely on the mathematics of cooperative games.

In a previous book, *Evolution's Rainbow*,[1] I offered a survey of diversity in gender and sexuality focusing on animals, together with a brief mention of humans across cultures and history. As I was writing *Evolution's Rainbow*, I became increasingly critical of how this diversity is ignored in biology curricula worldwide and critical of the language and theories purporting to describe and explain this diversity. The theory to account for sexual behavior in evolutionary biology is called "sexual selection," a topic that originates with Darwin's writings in 1871.[2] I concluded that Darwin's sexual-selection theory was completely false and needed to be replaced by some new and equally expansive theoretical system. I termed the replacement theory *social selection* but did little more than sketch a few points that such a new theoretical system might contain. I criticized the established theory and promised a new one someday.

Since 2004, my students and I have been publishing papers that develop mathematical models for issues such as why sex evolved, why the male/female binary evolved at both the gametic and whole-organism levels, whether a male and female are necessarily in conflict, and why males and females have offspring outside their pair bonds and raise young they have not parented. All these issues are central to understanding the reproductive social life of animals.

The topics of diversity in gender and sexuality that figured so prominently in *Evolution's Rainbow* receive little attention here, because a theory for such diversity depends on getting the foundational theory correct to begin with. Instead, the issue we face is whether sexual-selection theory offers a correct starting point for understanding *anything* having to do with reproductive social behavior, anything from peacock tails, to the worms robins feed their nestlings, to homosexuality. I don't think so.

Important and interesting as sexual selection may be in its own right, a still greater concern is the overall message that evolutionary biology imparts to the world. This book's title, *The Genial Gene*, alludes to the

1. Joan Roughgarden, *Evolution's Rainbow: Diversity, Gender and Sexuality in Nature and People* (Berkeley: University of California Press, 2004).

2. Charles Darwin, *The Descent of Man, and Selection in Relation to Sex* (Princeton: Princeton University Press, 1871 [facsimile ed]).

book, *The Selfish Gene*, written by Richard Dawkins in 1976[3] that extended and brought to general attention G. C. Williams' critique of group selection.[4] I remember teaching from *The Selfish Gene* when it first appeared and noticed the appeal that a naturalized doctrine of selfishness has to certain students and to those in the general public who, for example, identify with Ayn Rand's writings that celebrate the ethic of individualism.[5] This selfishness is now thought to be "nature's way" and evolutionary biology is thought to authorize the truth of selfish behavior throughout the living world. Evolutionary biology presently explains what little kindness and cooperation it wishes to acknowledge using work-around theories called *kin selection*[6] and *reciprocal altruism*.[7] These are theories whose purpose, as a proponent once told me, 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.

The selfish-gene philosophy is what I term *neo-Spencerism*. It claims to represent neo-Darwinism, which is what Darwinism has been called since genes were added to Darwin's original theory. However, the writings from the founders of neo-Darwinism, such as mathematical geneticists R. A. Fisher,[8] J. B. S. Haldane,[9] and S. E. Wright[10] in the 1930s and later, are relatively free of ideology. Similarly, Darwin's writings are relatively free of ideology compared to those of Herbert Spencer who coined the phrase, "survival of the fittest,"[11] which has become so emblematic of

3. Richard Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 1976).

4. George C. Williams, *Adaptation and Natural Selection*. Princeton: Princeton University Press, 1966.

5. Ayn Rand, *Atlas Shrugged* (Signet, 1957); Ayn Rand, *The Virtue of Selfishness: A New Concept of Egoism* (Signet, 1961).

6. Kin selection refers to an animal increasing its genes in the next generation by helping a close relative.

7. Reciprocal altruism refers to one animal helping another in expectation of the action being reciprocated some time later.

8. Ronald A. Fisher, *The Genetical Theory of Natural Selection* (Oxford: Oxford University Press, 1930).

9. J.B.S. Haldane, *The Causes of Evolution* (London: Longmans, Green and Co., 1932).

10. Sewall Wright, *Evolution and the Genetics of Populations,* vol. II of *The Theory of Gene Frequencies* (Chicago: University of Chicago Press, 1969).

11. Herbert Spencer, *The Principles of Biology,* vol. 1 (London: Williams and Norgate, 1864), 444.

Darwinism. The neo-Spencerists publicize "sexual conflict" as extending the selfish-gene metaphor into reproductive social behavior, including the "natural" roles for each gender and sex. Just as Spencer exaggerated and politicized the writings of Darwin, neo-Spencerists exaggerate and politicize the writing of neo-Darwinism's founders. They push selfishness and sexual conflict as the social message of neo-Darwinism just as Spencer pushed survival of the fittest as the social message of Darwinism.

Thus, the challenge I pose to sexual selection theory with its present-day embrace of the selfish gene and sexual conflict is important beyond understanding how many worms each bird brings to its nestlings and why the peacock has a colorful tail. What is being challenged is the scientific validity of a world view that naturalizes selfishness and sexual conflict.

When you hear two birds call in the morning, do you think they are lying to one another, planning how to cheat and steal from each other? Or could you think they may be coordinating their activities for the day's labor? The neo-Spencerists think the matter is already settled—birds, like the rest of the creatures in nature, supposedly spend their days lying, cheating, and stealing from one another.

In contrast, I think the matter is far from settled. 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. Well, I challenge the neo-Spencerists to be the scientists they claim to be, to engage and entertain alternative hypotheses objectively without descending to the personal and homophobic rebukes that have characterized their discourse so far.[12]

The sexual-selection theory underwrites "genetic classism" by naturalizing a mythical urge on the part of females to locate and sleep with males who have the best genes. Sexual selection is a narrative of genetic entitlement. I think the practicality of an egalitarian society

12. Cf. documentation in: Joan Roughgarden, "Challenging Darwin's Theory of Sexual Selection," *Daedalus* 136 (2):1–14 (2007); UK homophobic backlash in: C. McKechnie and D. Shuker, *Journal of Literature and Science* 1 (1):75–76 (2007); and recent governmental summaries of UK homophobia in: www.pfc.org.uk/files/reporting_homophobia_in_the_health_sector.pdf and www.pfc.org.uk/files/ eurostudy.pdf.

depends on whether a rational rejection exists for sexual selection. If sexual selection is indeed true, then so be it; and the prospect of an egalitarian society is an unrealistic mirage. Alternatively, if sexual selection is not true, it should not be left to die in secret, but should be explicitly discredited lest sexual selection remain on the books as an obstacle to social justice.

In 1976 when Richard Dawkins wrote *The Selfish Gene*, he was primarily debunking group selection while emphasizing individual selection as the more important route to evolutionary success. He was criticizing a familiar narrative at the time that accounted for the evolution of traits by appeals to group or species benefits. I agree with Dawkins that individual selection is more significant to evolutionary success than group selection, and I respect his contributions concerning that point. I, too, seek evolutionary explanations that rely on individual selection and do not appeal to group selection. Instead, my challenge concerns the scientific accuracy of the philosophical world view that the phrase "selfish gene" has come to represent.

For example, *The Selfish Gene* publicizes a view of nature emphasizing competition: "We are survival machines–robot vehicles blindly programmed to preserve the selfish molecules known as genes," Dawkins writes. He continues with, "Our genes made us. We animals exist for their preservation and are nothing more than their throwaway survival machines. The world of the selfish gene is one of savage competition, ruthless exploitation, and deceit." In *River Out of Eden*,[13] Dawkins writes, "The universe we observe has precisely the properties we should expect if there is, at bottom, no design, no purpose, no evil and no good, nothing but blind pitiless indifference." And he states in the book, *Devil's Chaplain*,[14] "Blindness to suffering is an inherent consequence of natural selection. Nature is neither kind nor cruel but indifferent." These books develop a philosophy of universal selfishness, conflict, and lack of empathy as though revealed through evolutionary biology.

13. Richard Dawkins, *River Out of Eden: A Darwinian View of Life* (Basic Books, 1995).

14. Richard Dawkins, *A Devil's Chaplain: Reflections on Hope, Lies, Science, and Love* (Houghton Mifflin, 2003).

The issue before us is not whether this philosophy is appealing or repugnant. The issue is whether it is a true and accurate account of nature, of what the birds and bees around us are doing—whether their lives are really selfish and filled with uncaring sexual conflict.

This book is planned for release in 2009, the year of what promises to be a grand bi-centennial celebration of Darwin's birthday on February 12, 1809. Yet, among the anticipated horde of books praising the Darwinian "triumph," one will be able to discern critiques of some parts of Darwin or of later work extending Darwinism.

One critique, associated with Eva Jablonka and Marion Lamb,[15] Mary Jane West-Eberhard,[16] Massimo Pigliucci,[17] and Sean B. Carrol[18] challenges the genetic assumptions of neo-Darwinism, not Darwinism itself. This challenge does not extend to Darwin's writings, because Darwin wrote before genes were discovered, and Darwinism does not take a position on the mechanism of inheritance. This challenge does argue that the "new synthesis" of Ernst Mayr[19] and others in the 1940s to 1960s, which applied neo-Darwinism to systematics and paleontology, is inadequate in light of today's molecular and developmental genetics. This critique arises from evolutionary-developmental biology, or evo-devo for short, and seeks to update neo-Darwinism—indeed Eva Jablonka told me she has at times described herself as a Darwinist, but not a neo-Darwinist.

15. Eva Jablonka and Marion J. Lamb, *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* (Cambridge: The MIT Press, 2005); E. Jablonka, "From Replicators to Heritably Varying Phenotypic Traits: The Extended Phenotype Revisited," *Biology and Philosophy* 19 (2004): 353–375; cf. also: Richard Dawkins, "Extended Phenotype–But Not Too Extended. A Reply to Laland, Turner and Jablonka," *Biology and Philosophy* 19 (2004): 377–396.

16. Mary Jane West-Eberhard, *Developmental Plasticity and Evolution* (New York: Oxford University Press, 2003); cf. also: Eva Jablonka, "Genes as Followers in Evolution–A Post-synthesis Synthesis? A Review of Mary Jane West-Eberhard, Developmental Plasticity and Evolution, 2003," *Biology and Philosophy* 21 (2006): 143–154.

17. Massimo Pigliucci, *Phenotypic Plasticity: Beyond Nature and Nurture* (Baltimore: The John Hopkins University Press, 2001); Massimoo Pigliucci, "Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes," *Ecology Letters* 6 (3): 265–272 (2003).

18. S. B. Carroll, "Evolution at Two Levels: On Genes and Form," *PLoS Biol* 3(7): e245 doi:10.1371/journal.pbio.0030245 (2005).

19. Ernst Mayr, *Animal Species and Evolution* (Cambridge: Harvard University Press, 1963).

Although the new synthesis of the 1940s needs some far-reaching revision to take account of contemporary genetics and developmental biology, it has made a long-lasting and likely permanent contribution in changing how the biological categories are understood. The original biological classification system of Linnaeus envisioned that a species could be identified with a "type" specimen that could be taken as definitional. One could go to a research museum like the British Museum in London or the American Museum in New York, open a drawer, and pull out a specimen of say, a robin, and it would instantiate the definition of "robin-hood." Any other specimen of a bird could be compared to the type specimen to determine if it was a robin too. If the specimen didn't exactly match, it was imperfect and not quite a "true" robin. But since the new synthesis, a species has been identified with a *sample* from a population. The museum drawer now contains a dozen or more robins that collectively define robin-hood. So, an unknown specimen now is compared to the collective sample to see if it falls within the range of variation naturally exhibited throughout the sample. If the specimen fits within the sample, it's a robin, plain and simple.

This denial of any "type" specimen carries over to within-species categories, too. There is no type specimen of a race, gender, or sexuality profile. Even though the rejection of what Ernst Mayr termed *typological thinking* has been foundational to evolutionary biology for nearly 75 years now, this insight has yet to be fully appreciated in medicine, especially pediatrics, urology, psychology, and psychiatry. These medical disciplines persist in attempting to "diagnose" persons into human categories that to an evolutionary biologist's eye are purely social constructs without any possibility of biological reality or precision. In biology, nature abhors a category. In biology, nature consists of rainbows within rainbows within rainbows . . .

In contrast, my sexual-selection critique does go back to what Darwin wrote, and how he conceived of social relations between males and females. Nonetheless, its replacement, social selection, is an evolutionary theory, too. Sexual selection and social selection both lie under the common umbrella of evolutionary biology, but offer very different accounts of what it takes to achieve evolutionary success within the gene

pool of any species that possesses a social system, which is all of them, including in a sense, plants.

Finally, I have also pressed a third critique that pertains to evolutionary biology generally, and not Darwin specifically, and that has been also made by many biologists over the years. Evolutionary biology awaits an extended discussion about what an "individual" is.[20] Who counts as an individual seems obvious when thinking of ourselves, or our pets, livestock, or other organisms who become detached from their parents at birth. But individuality is not so clear cut in many other species. A grove of poplar trees consists of many trunks springing from one seed—what is the individual, a single tree trunk or the entire grove? Or consider a strawberry plant, or beach grass on a sand dune—these reproduce with runners, either above or below the ground. What does survival of the fittest mean when we can't say exactly who it refers to—the fittest tree trunk or the fittest grove of trees?

Without explicitly saying so anywhere, biologists define an individual as an entity containing one genome in one body. The problems turn up in species where one genome gives rise to multiple bodies, as in poplar trees, strawberries, and beach grass, or where multiple genomes reside within a single body, as in the endosymbiosis of algae with fungi in lichens, of algae with corals, and of algae with giant coral-reef clams. And then there are clusters of distinct individuals who are bunched together into a single functional unit, such as the Portuguese Man-O-War jellyfish, which consists of many separate polyps attached to one another that float around together like a spaceship in the ocean. In this case, survival of the fittest means survival of the fittest cluster, which then trickles down somehow to the prosperity of the individual polyps within the cluster.

Defining individuality has long been a problem for mycologists.[21] A hypha is a thin tube surrounded by a wall. Typically, hyphae are divided

20. Joan Roughgarden, *Evolution and Christian Faith: Reflections of an Evolutionary Biologist* (Washington: Island Press, 2006), 71–78.

21. Alan Rayner and Nigel Franks, "Evolutionary and Ecological Parallels Between Ants and Fungi," *TREE* 2 (1987): 127–133; Alan D.M. Rayner, "The Challenge of the Individualistic Mycelium," *Mycologia* 83 (1): 48–71 (1991); A. D.M. Rayner, *Degrees of Freedom Living in Dynamic Boundaries* (Imperial College Press, 1997).

into cells by cross-walls called septa. Septa usually have pores in them large enough for ribosomes, mitochondria, and sometimes even nuclei to flow among cells. Therefore, a hypha is like a conduit through with all the subcellular players can traffic back and forth. A mycelium is a branching network of hyphae, and these are found in soil and on, or in, all the substrates where fungi live. Fruiting bodies like mushrooms might grow up out of the mycelium. A mycelium may be too small to see or may be gargantuan. A 2,400-acre site in eastern Oregon had a contiguous growth of mycelium estimated to be 2,200 years old.

Many phenomena are already known, and more are being discovered, about how fungi interact with one another when mycelia contact. They may fuse and exchange nuclei or they may repulse each other. The cells between septa may contain multiple nuclei that are identical to one another or that may be genetically different. It's hard to find a vocabulary to describe the physiology within, and interaction between, fungal mycelia. I like to compare a fungal mycelium to a termite nest. Perhaps you may have seen a termite nest outdoors together with the system of corridors that the termites construct out of mud. If you open a crack in one of the corridors, you can see termites moving back and forth through their tunnels. A mycelium is similar, but it's the nuclei and other cellular organelles that traffic back and forth. In this case, the nuclei can be regarded as the "individuals," but these individual share space and function with other types of individuals, the mitochondria, and other organelles. In comparison to fungi, the plants and animals that have only a single nucleus per cell are special cases, like one house per lot in suburban living rather than a duplex, townhouse, commune, and other living arrangements preferred across diverse human cultures and locales.

Biologists working with social insects, the bees, wasps, ants, and termites, have also long puzzled about what an individual means. The common picture of a social insect nest consisting of a single queen plus workers has long been explained by kin-selection theory. I can recall teaching this theory as though gospel during the 1970s, and it figures so prominently in *The Selfish Gene*. Worker-ants are daughters of the queen-ant and share a high genetic relationship to her because of a special genetic system that bees, wasps and ants happen to have (called haplo-diploidy).

Because of an unusually high genetic relationship between daughter and mother in these species, worker-ants can send copies of their own genes into the next generation more effectively *via* the route of helping their mother to produce offspring rather than bothering to produce offspring by themselves.[22] This idea is fine, provided a nest really does consist of one queen together with her daughters as the workers.

However, social insect nests in many species form a huge distributed system with often unrelated multiple queens and cohorts of workers with differing parentage.[23] An extreme example is the "super-colony" of the red wood ant on a coastal plain in Hokkaido, which has 306 million workers and over a million queens living in 45,000 interconnected nests across a territory of 2.7 km^2. [24] These distributed entities in which the individual is poorly defined defy any ready application of kin-selection theory to explain the often cooperative social dynamics. Kin-selection is not incorrect, merely inadequate.

Although the forms of life just mentioned are well known to invertebrate zoologists and botanists, and are well described in their textbooks, evolutionary biology and its textbooks simply avoid such species in which the definition of an individual is problematic. The seeming clarity with which evolutionary biology seems to bespeak of individualism in books like *The Selfish Gene* is illusionary because only a subset of the species is being addressed by evolutionary studies, namely, the subset in which the definition of an individual is not problematic. Belief that evolutionary science somehow reveals the naturalness of individualism is circular, because it is based on species chosen in part because they do not challenge an individualistic perspective.

22. W. D. Hamilton, "The Genetical Theory of Social Behavior. I. II," *J Theor Biol* 7 (1964): 1–52.

23. Bert Hölldobler and Edward O. Wilson, "The Number of Queens: An Important Trait in Ant Evolution," *Naturwissenschaften* 64 (1977): 8–15; Laurent Keller, "The Assessment of Reproductive Success of Queens in Ants and Other Social Insects," *Oikos* 67(1): 177–180 (1993); David C. Queller et al., "Unrelated Helpers in a Social Insect," *Nature* 405 (2000):784–786.

24. S. Higashi and K. Yamauchi, "Influence of a Supercolonial Ant *Formica (Formica) yessensis* Forel on the Distribution of Other Ants in Ishikari Coast," *Jap J Ecol* 29 (1979): 257–264; S. Higashi, "Polygyny and Nuptial Flight of *Formica (Formica) Yessensis* Forel at Ishikari Coast, Hokkaido, Japan," *Insectes Sociaux, Paris* 30 (3): 287–297 (1983).

We can't continue indefinitely to neglect or downplay species in which the definition of an individual is problematic. After all, there are many thousands of species like poplars, beach grass, mushrooms, giant clams, corals, tunicates, bryozoans, Portuguese Men-O-War, and so forth whose evolution we'll have to understand someday. But more interestingly for the purposes of this book, social connections are just as important as material connections. Sure, beach grass stems share a *material* connection through their roots. But members of a pack of wolves or a pod of whales share a *social* connection that binds them into a unit, a team, every bit as real as the material connections that bind popular trees together.

The lack of clarity about what defines an individual in biology brings us to the fundamental problem with the selfish-gene metaphor—it overlooks the issues of decomposability and teamwork.

Take two robins, a male and female, who build a nest together. An interview in *The Guardian* on February 10, 2003, describes Richard Dawkins who "wanders over to the other side of the room and returns with a bird's nest that he picked up in Africa. 'It's clearly a biological object.' His eyes light up. 'It's clearly an adaptation. It's a lovely thing.' He says that birds do not need to be taught to make nests, they are genetically programmed to do so." Whether a bird's ability to make a nest is genetically endowed is not the point. The point is whether one or two birds cooperated to make it. Dawkins sees the evolution of nest-building ability as another success story for some selfish genes. In fact, the nest results from the *relationship* developed by the male and female during courtship. Both bring twigs to build the nest. The success of the genes in either bird is zero if the other doesn't do their job, and so the success of the nest is attributable to the relationship of trust established between both birds. Therefore, the genes for nest-building do represent an evolutionary success story, but not success because of selfishness. The success of the nest-building genes in any one robin rests on their ability to work with the genes in another robin.

Moreover, the success of the nest is not decomposable to a sum of the twigs brought by each, because half a nest is useless. No one has yet figured out a useful way to decompose team achievements into individual contributions. Does anyone really think a pitcher is the one who wins a

baseball game, forgetting about the hitters and fielders? It's the team who wins or not. In the 30 years since the selfish-gene metaphor has gained traction as a popularization of neo-Darwinian thought, it has yet to emerge as a scientifically operational concept because of the decomposability problem.

Still, at this point a selfish-gene advocate typically retorts that a robin who cooperates with another robin in building a nest is helping itself, and so can be thought of as selfish after all. But that vacates the meaning of selfish. "Selfish gene" and "successful gene" are not the same thing. Think of it this way. Suppose a species has 25,000 genes in it and suppose 200 of them increase in frequency from one generation to the next while another 200 of them decrease. Why? If the increase is due to natural selection and not chance fluctuation, then do the 200 increase because they cooperate more effectively with each another than the other 200 who decline, or do the 200 increase because they interfere with, harm, or outcompete the other 200 for scarce limiting resources? No one knows. It's an open empirical question whether effective cooperation among genes versus effective competition between them underlies most evolutionary progress. But to stipulate that evolutionary success equals selfishness means we can't ask the question of which, cooperation or competition, is the more common route to evolutionary success.

The explanation for why the male and female robins cooperate to build a nest together cannot be subsumed under kin selection, reciprocal altruism, or group selection.[25] The male and female robins are usually not brother and sister or another close relative, so kin selection does not apply. The female and male robins are not exchanging altruistic acts that directly help each other as individuals, so reciprocal altruism does not apply. And a robin's nest does not bud off other nests, so group selection does not apply either—pairs don't reproduce other pairs, or live or die as a pair.[26]

25. Group selection is the differential survival and/or reproduction of groups and is contrasted with individual selection, which is the differential survival and/or reproduction of individuals.

26. A more extended discussion of the relation between kin selection and group selection appears toward the conclusion of Chapter 9.

Instead, the male and female robin are cooperating because they have a shared interest—together they form what might be called an "evolutionary household," a kind of evolutionary team, and they share a common bank account of evolutionary fitness consisting of the genes from both contained in the offspring they jointly raise.

"Cooperative teamwork" is a distinct principle from the older ideas of kin selection, reciprocal altruism, and group selection. In kin selection and reciprocal altruism, each individual acts solely from their own viewpoint—the worker-ant exploits the queen-ant to produce eggs that carry her genes rather than bother producing the eggs herself. Meanwhile, producing eggs is the queen-ant's evolutionary objective as well. The worker and queen share no common goal; they merely enjoy an independent coincidence of two individual goals. In cooperative teamwork, the evolutionary payoff is earned by the team as a unit through coordinated actions by its members in pursuing a team goal, and the payoff from team success is then distributed, perhaps unequally, among the team members with no individual earning anything unless their team succeeds. Cooperative teamwork is not an independent coincidence of individual interests, but the acceptance of a team goal and working together to attain that goal. Yet, effectiveness at cooperative nest-building evolves through ordinary individual selection, not group selection, because the route to evolutionary success for each *individual* robin is through cooperation with the other. On the other hand, cooperative teamwork is not group selection either, but individual selection with evolutionary success as an individual being attained through coordinated activity in pursuit of a team goal.

Now let's pass to the critique of sexual selection and to the development of its replacement.