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Inclusive Fitness Theory from Darwin to Hamilton

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ONE of the central dogmas of modern behavioral ecology is that blood kinship plays a critical role in understanding the evolution of social behavior, particularly of costly social behavior such as altruism and cooperation. But it was not always so, and what I would like to do in this *Perspectives* is provide some historical context that led up to William Hamilton's seminal work developing inclusive fitness theory. The story begins, not surprisingly, with Charles Darwin.

The worker bees that sacrifice themselves to protect their hives—the ultimate example of animal altruism—were deeply troubling to Darwin. If increased reproduction is the currency of natural selection, then altruists should disappear—and fast. But they did not disappear, and Darwin was so puzzled by this that he spoke of altruism as a problem that he feared was "one special difficulty, which at first appeared to me to be insuperable, and actually fatal to the whole theory" (Darwin 1859, p. 236). Eventually, however, Darwin came up with an explanation.

Since sterile worker bees were helping their blood relatives—especially the queen—Darwin hypothesized that natural selection might favor altruism at the level of blood kin. In a section of *On the Origin of Species* entitled "Objections to the theory of natural selection and instinct: neuter and sterile insects," Darwin proposes that the problem of natural selection producing sterile castes that often risk their lives to protect others "disappears when it is remembered that selection may be applied *to the family*, as well as the individual and may thus gain the desired end" (Darwin 1859, p. 204). Blood kinship, and interactions among relatives, it turned out, was the key to solving Darwin's problems with both social insect sterility and altruism.

One hundred and four years later, biologist William Hamilton would formalize Darwin's idea, but the path from Darwin to Hamilton was not smooth (Dugatkin 2006). That fact that it was not is not surprising. The nature of altruism makes it all too easy to drift from a scientific to a political, philosophical, and even a religious approach to this subject. Studying the structure of an atom is not personal, and neither is studying, for example, night vision in mammals. Studying altruism can be personal, however, because we all want to understand the origins of goodness. And it certainly was personal for the next two figures in the story of blood kinship and altruism—Thomas Henry Huxley and Peter Kropotkin (Woodcock and Avakumovic 1950; Desmond 1994).

HUXLEY AND KROPOTKIN

Huxley, who coined the moniker "Darwin's Bulldog" for himself, was delighted to be the public face of evolution in Victorian England. He relished the chance to spread Darwin's ideas near and far, going so far as to write to Darwin on the eve of the publication of *On the Origin of Species* that: "As to the curs which will bark and yelp, you must recollect that some of your friends, at any rate, are endowed with an amount of combativeness which . . . may stand you in good stead. I am sharpening up my claws and beak in readiness. . . . prepared to go to the stake, if requisite" (Huxley 1901, pp. 188–189).

With respect to the question of altruism and blood kinship, Huxley pulled no punches: in his 1888 essay entitled "The struggle for existence," Huxley was brutally frank: "From the point of view of the moralist, the animal world is on about the same level as the gladiator's show. . . . Life was a continuous free fight, and beyond the limited and temporary relations of the family, the Hobbesian war of each against all was the normal state of existence" (Huxley 1888, pp. 163–165). For Huxley, altruism should be a rare event in the natural world, but when it occurred, it should be between blood relatives.

Peter Kropotkin, ex-page to the Czar of Russia and a naturalist who spent 5 years studying natural history in

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Siberia, took issue with Huxley's views (Kropotkin 1899; Todes 1987, 1989). In Siberia, Kropotkin believed that he saw altruism in every species that he came across, and all this altruism, as Kropotkin saw it, was divorced from blood kinship. "Don't compete!" Kropotkin wrote in his influential book *Mutual Aid*. "That is the watchword which comes to us from the bush, the forest, the river, the ocean. Therefore combine—practice mutual aid!" (Kropotkin 1902, p. 75). In one sense, the Huxley–Kropotkin debate was important, if, for no other reason, than that Huxley was arguably the most famous scientist in Europe and Kropotkin was the most famous anarchist in the world. On the other hand, their arguments were more philosophical than scientific. There were no experiments, and neither of them ever formalized a theory on the connection between blood relatedness and altruism—via mathematical model or otherwise—each just knew in his heart that he was right. Huxley and Kropotkin translated their sense of purpose on these matters into statements that went far beyond what the science of their day could support.

HALDANE, FISHER, AND WRIGHT

The mathematical models tying blood kinship and altruism *almost* came to fruition during the modern synthesis. J. B. S. Haldane, Sewall Wright, and Ronald Fisher all came tantalizingly close, but stopped short. For example, legend has it that in a pub one evening Haldane told his friends that he would jump into a river and risk his life to save two brothers, but not one, and that he would jump in to save eight cousins, but not seven. Haldane was infamous for such quips, but the point here is that this particular quip makes sense only in terms of gene counting and hints at the logic that would eventually underlie inclusive fitness theory.

Haldane did not formalize his ideas on blood kinship and altruism until publication of his classic book, *Causes of Evolution*, and then again later in an article entitled "Population genetics" (Haldane 1932, 1955). He addressed kinship and altruism in *Causes of Evolution* while trying to make sense of genes that lower the fitness of the individual in which they reside, but increase the fitness of others in their society. For Haldane, such genes were doomed to be "extinguished by natural selection in large societies." In the appendix to *Causes*, where he could be a bit more technical, Haldane argued that altruism can spread in small groups if "the genes determining it are borne by a group of related individuals whose chances of leaving offspring are increased by the presence of these genes in an individual member of the group whose own private viability they lower" (Haldane 1932, p. 119). Like the case of the quip in the pub, Haldane's message here is clear: if a gene coding for altruism benefits blood relatives, it could, in principle, spread through a population by the process of natural selection.

Haldane deferred a more precise description of how kinship affects altruism to his 1955 article on population genetics, where he asks the reader to imagine the following scenario in a small population:

> Let us suppose that you carry a rare gene that affects your behavior so that you jump into a flooded river and save a child, but you have one chance in ten of being drowned, while I do not possess the gene, and stand on the bank and watch the child drown. If the child's your own child or your brother or sister, there is an even chance that this child will also have this gene, so five genes will be saved in children for one lost in an adult. If you save a grandchild or a nephew, the advantage is only two and a half to one. If you only save a first cousin, the effect is very slight. If you try to save your first cousin once removed the population is more likely to *lose this valuable gene* than to gain it. . . . It is clear that genes making for conduct of this kind would only have a chance of spreading in rather small populations when most of the children were fairly near relatives of the man who risked his life" (Haldane 1955, p. 44).

This paragraph is a precursor to modern evolutionary thinking on kinship and altruism. Yet Haldane did not take the next step and develop a general equation that captured these costs and benefits and their relationship to kinship. And, in particular, he made no attempt to understand how natural selection might act to maximize rules about dispensing altruistic acts among kin. This is somewhat remarkable, because Haldane made his career developing mathematical models of natural selection. Yet, aside from the appendix in *Causes*, on this one issue Haldane seemed to skip the mathematics.

Before publishing his masterful book, *The Genetical Theory of Natural Selection*, Fisher apparently had little to say about how kinship might affect the evolution of altruism, although he had published extensively on how to calculate degrees of genetic relatedness between individuals living in various types of populations (Fisher 1918, 1930, 1958, 1999). Fisher's primary sortie into the relationship of altruism and genetic relatedness appears in a section of *The Genetical Theory of Natural Selection* entitled "The evolution of distastefulness." For Fisher, the evolution of most defensive mechanisms in insects was easily explainable. Fisher, however, puzzled over a related phenomenon, namely "the process by which nauseous flavours as a means of defence, have been evolved" (Fisher 1958, p. 177). And it was these "nauseous flavours" as defense mechanisms that led Fisher into directly tackling questions related to altruism and kinship.

Fisher had learned from entomologist Edward Bagnall Poulton that the body of many adult insects was tough enough to survive a predator's initial bite. But what about distastefulness in insect larvae, who have much softer outer skeletons and could not survive a predator's first bite? Here, Fisher argued that the effect of distastefulness "will certainly be to give the increased protection especially to one particular group of larvae, probably brothers and sisters of the individual attacked" (Fisher 1958, p. 178). If a predator responded to the noxious taste of a prey item and, in turn, avoided ingesting the kin of the noxious (young) victim, then even if the larvae died, natural selection at the level of the kin group could favor possession of such distastefulness in the prey species. Fisher seemed on the verge of a mathematical model of kinship and altruism when he next noted that by saving the life of a nearby sibling, the deceased (distasteful) individual receives a genetic benefit since it is related to its sibling. Fisher argued that when a predator abandons a site after ingesting a distasteful individual, *many* of that individual's sibs might be saved, and hence the genetic benefit to the deceased could be very substantial. Natural selection would then favor life-sacrificing altruistic traits such as distastefulness. But then Fisher, aside from a discussion of bravery, altruism, and kinship in humans, drops the whole matter.

Sewall Wright—the very man who developed *r* as the measure of genetic relatedness—failed to build a mathematical model linking genetic relatedness and altruism. This is especially odd because Wright did build a group selection model of altruism, but he never linked that model to his work on genetic relatedness.

All of this begs the question—Why is it that none of the founders of mathematical population genetics built a model linking kinship and altruism? It may simply have been that Haldane, Fisher, and Wright thought the subject matter uninteresting, but that seems unlikely, given that each did take the time to write on relatedness and altruism in the first place. Another possibility is mathematical arrogance on the part of Haldane, Fisher, and Wright. Perhaps they were convinced that anyone with any mathematical know-how should be able to easily use their published material on saving drowning relatives or protecting insect larvae and immediately translate these in their heads to a mathematical model of kinship and altruism. This arrogance hypothesis, however, does not stand up to closer scrutiny. Haldane, Fisher, and Wright were in a fierce competition to produce the first comprehensive group of mathematical models of evolution by natural selection. If any one of them had thought of an explicit model of kinship and altruism, they likely would have published it.

My colleagues Kern Reeve and Thomas Seeley (both at Cornell) suggest that since none of the three founders of population genetics spent any amount of time in the field observing altruism and the role kinship plays in promoting it, perhaps they all lacked the natural history experience needed to properly model the phenomenon. This is certainly an intriguing possibility. Alan Grafen at Oxford University speculates that because the economic-based approach to evolution and behavior that would come to dominate work in this area in later decades was not yet in place in the days of Haldane, Wright, and Fisher, there was no framework upon which to build a mathematical model of altruism via kinship. Haldane and Wright, for instance, did not think of natural selection as an optimization process (although Fisher did) and hence would not have thought about developing a model for how selection might optimize any rules with respect to kin-based altruism. In addition, for the most part, Haldane, Fisher, and Wright did not think about the costs and benefits of altruism as variables and, without that, a mathematical model of kinship and altruism would be hard to envision.

We can only speculate as to why Haldane, Fisher, and Wright did not build explicit models of kinship and altruism. What we do know, however, is that when William D. Hamilton published his seminal models of altruism and kinship in 1963 and 1964, he made his debt to Haldane, Wright, and Fisher—the grand triumvirate, as he called them—very clear (HAMILTON 1963, 1964).

W. D. HAMILTON

Bill Hamilton's early interest in natural history developed into a burning passion to study the evolution of behavior. In the late 1950s, he began his undergraduate education at Cambridge University. As a young man set on studying biology and, in particular, natural history, evolution, and genetics, Hamilton was disappointed by what he saw at Cambridge. Despite the fact that the modern synthesis was well under way, Hamilton found that "many Cambridge biologists seemed hardly to believe in evolution or at least seemed to be skeptical of the efficacy of natural selection" (HAMILTON 1996, p. 21).

One day while he was studying at Cambridge's St. Johns Library, Hamilton came across *The Genetical Theory of Natural Selection.* Hamilton "immediately realized that this was the key to the understanding of evolution" (HAMILTON 2001, p. 543). He became a self-admitted "Fisher freak" and immersed himself in *The Genetical Theory of Natural Selection* to the exclusion of everything else, including his course work at Cambridge (HAMILTON 2001).

Hamilton was enrolled as a genetics major at Cambridge, and the degree program in genetics required that students take some elective courses in other departments. He thought that a course in social anthropology might satisfy both Cambridge's requirements and his own interest in human altruism. To learn more about the social anthropology course offered at Cambridge, he spoke to the course's instructor, Edmund Leach. Leach believed that *all* human behavior was culturally derived and that genetics had no bearing on the behavior of our species. Once Leach realized that Hamilton was interested in studying evolution, genetics, and altruism, he became unreceptive to anything the young man had to say.

The reaction of the Department of Genetics to Hamilton's idea of taking a class in social anthropology was almost as unreceptive. The geneticists told him that they believed that taking a course social anthropology was on a par with a class in poetry. The whole episode did more than sour Hamilton on Cambridge University—it caused him to reconsider a career in science. "I am beginning to find Cambridge intolerably oppressive," Hamilton wrote to his sister Mary in November of 1959. "I think I will give up the hope of making headway against all this," he continued, "and take up school teaching and do my research on my own—after all it involves hardly anything but reading."

After graduating from Cambridge University, Hamilton reconsidered graduate studies in genetics, evolution, and behavior. He eventually settled on doing his dissertation jointly at University College and the London School of Economics and began to piece together his ideas on evolution, kinship, and altruism. In so doing, he realized that the evolutionary biologist is both blessed and cursed with "a fourth intellectual pigment of the retina capable of raising into clear sight patterns of nature and of the human future that are denied the majority of his fellows . . ." (HAMILTON 1996, p. ix).

Hamilton published his first scientific paper, "The evolution of altruistic behavior," in 1963 in The American Naturalist (HAMILTON 1963). He opened this three-page paper with a statement that later would become the bedrock for all of sociobiology: "It is generally accepted that the behaviour characteristic of a species is just as much the product of evolution as the morphology." But, Hamilton quickly added, there were some kinds of behavior that could not easily be explained by classic evolutionary thinking, "in particular . . . any case where an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own" (HAMILTON 1963, p. 354). To address these sorts of behavior, Hamilton built the first "inclusive" model for the evolution of altruism.

Using Wright's "coefficient of relationship," r, as his measure of genetic relatedness, Hamilton added in the costs (c) and benefits (b) of altruism to his model. The importance of adding b and c to his model was that it allowed Hamilton to take an economic approach to how natural selection might maximize fitness and still allow for the evolution of altruism. In his graduate days at the London School of Economics, Hamilton must have been exposed often to this sort of cost–benefit optimization analysis. But applying it to an evolutionary problem—that of altruism—was a watershed moment for the field of evolution and behavior.

In Hamilton's model, natural selection favors the gene for altruism whenever $r \times b > c$. This equation has become known as Hamilton's Rule and can be distilled down to this: if a gene(s) for altruism is to evolve, then the cost (c) of altruism must somehow be balanced by compensating benefits to the altruist. In Hamilton's model, the cost is balanced by benefits (b) accrued by blood relatives of the altruist, because relatives *may* carry the gene for altruism as well. But relatives have only *some probability*, r, of carrying the gene in question, and so the benefits received must be weighted by that probability.

Hamilton's model filled a psychological void for those studying evolution and behavior. Up until 1963, evolutionary biologists who focused on behavior suffered from what one might call "physics envy," in that they saw mathematical equations not only as tools that promote hypothesis generation and hypothesis testing, but also as objects that garner respect from other scientists. Very few such equations existed in the area of evolution and behavior before 1963, and none of them packed the punch of Hamilton's equation. Indeed, "The evolution of altruistic behavior was almost immediately eclipsed by another pair of Hamilton articles—"The genetical evolution of social behaviour. I and II"—published a year later (1964) in the Journal of Theoretical Biology (HAMILTON 1964). In these articles, Hamilton provided much more mathematical detail and discussed, at length, how his ideas could explain the evolution of social behavior.

Bill Hamilton was on his way from Brazil to Britain when "The genetical evolution of social behaviour," parts I and II, were published in the summer of 1964. During the 18 months leading up to the publication of his Journal of Theoretical Biology articles, Hamilton was out in the rainforests of Brazil doing what he loved to do best—study insects in the wild. So great was his passion for Brazilian insects that, in a short 1991 article called "My intended burial and why," Hamilton announced that, when he died, he wanted to be buried in the rainforest, where the giant Coprophaneaeus beetles "will enter, will bury, will live on my flesh; and in the shape of their children and mine, I will escape death" (HAMILTON 1991, p. 122).

Over time, Hamilton's work on kinship and altruism, along with his many other seminal contributions, would make him one of the leading evolutionary biologists of the twentieth century (GRAFEN 2004). But the late 1960s and early 1970s were not all that Hamilton had hoped they would be. With some notable exceptions, such as Richard Dawkins, E. O. Wilson, and Robert Trivers, until the mid-1970s not many people seemed to take note of Hamilton's kinship articles. One person who did notice, however, was an unknown genius named George Price.

GEORGE PRICE

Price's eclectic interests turned to evolutionary biology in 1966 when he took the cash that he received from an insurance settlement for a botched thyroid operation, bought a ticket on the *Queen Elizabeth*, and sailed to England to study evolutionary biology. Sometime in 1968, Price came across Hamilton's models on kinship and altruism and wrote Hamilton for a reprint. After he read Hamilton's altruism and kinship articles, Price was depressed. He had hoped that all goodness was somehow exempt from scientific analysis, but Hamilton's models seemed to demonstrate otherwise. After starting from scratch and proving to himself that

Hamilton's mathematics were accurate, it dawned on Price that Hamilton had actually *under*estimated the power of his own equations and that Hamilton's models could be used to study the evolution of spiteful behavior, as well as of altruistic behavior.

Price began with Hamilton's models and then developed a new way to model evolutionary change—a model that relied on covariance analysis. Using this covariance analysis, first introduced into evolutionary biology by Alan Robertson, Price found that when individuals were in groups with lots of blood kin, then a gene coding for altruism had a positive covariance with the number of offspring that an individual produced. What was new was Price's finding that if the average relatedness within groups is less than the average genetic relatedness within the population—that is, when individuals in groups are "negatively" related—then spiteful behavior can evolve.

Price's spite model, along with a complementary article by Hamilton, was published in Nature in 1970 (HAMILTON 1970; PRICE 1970). At virtually the same time that these articles appeared, George Price the atheist underwent a religious conversion. "On June 7th [1970] I gave in," Price told friends, "and admitted that God existed" (SCHWARTZ 2000, p. 56). As Hamilton remembered it, Price "believed that the discovery he had made in evolutionary theory was truly a miracle . . . God had given him this insight where he had no reason to expect it. It was ludicrous, he [Price] told me that he, a person who never understood or used statistics and had hardly known previously a covariance from a coconut, could have discovered the simple formula that should prove to be the most transparent yet found to partition and interpret the working of natural selection" (HAMILTON 1996, p. 323).

In December 1974, George Price spent a week with the Hamiltons, who had become his dear friends, and when he left, it was with the understanding that he would return shortly after New Year's Day. Sometime after he left the Hamilton home, Price became deeply depressed. On January 6, 1975, he slit his throat and committed suicide. Hamilton was charged with cleaning out Price's flat and described a bleak scene: "As I tidied what was worth taking into a suitcase, his [Price's] dried blood crackled on the linoleum under my shoes; a basically tidy man, he had chosen to die on the open floor, not on his bed" (HAMILTON 1996, p. 174).

ONWARD

Bill Hamilton's 1963 and 1964 inclusive fitness articles are easily the most cited articles in the entire field of behavioral evolution, and his work on altruism and kinship spurred endless dissertation projects and hundreds of published articles, both theoretical and empirical. When modern behavioral ecologists and sociobiologists are asked to mark the birth of the field, many respond by citing Hamilton's 1963 and 1964 articles. Of course, progress on kinship and altruism has continued from 1963 to the present, as Hamilton had hoped it would. And debate on these subjects continues as well—just as one might expect for ideas that fundamentally changed the way in which people thought about the evolution of behavior.

Hamilton's work led to his election to the Royal Society of London in 1980. He was also awarded the Royal Society's Darwin Medal (1988), the Scientific Medal of the Linnean Society (1989), the Zoological Society of London's Frink Medal (1991), the Kyoto Prize (1993), and the Royal Society of Sweden's Crafoord Award (1993) and received virtually every other accolade that could possibly be bestowed on an evolutionary biologist.

Because of his seemingly endless fundamental contributions to the discipline, evolutionary behaviorists looked to Bill Hamilton as a leader and a man who was expected to spend the last part of his life as an elder statesman in the field. But that was never to be. On March 7, 2000, after 5 weeks in a semicomatose state, 63-year-old William D. Hamilton died as a result of a massive hemorrhage following a very serious bout of malaria. Hamilton had been in the Congo testing the now-discredited hypothesis that HIV had initially spread from other primates to humans through a botched polio vaccination program undertaken in Africa during the 1950s (HOOPER 1999). He failed to find the evidence he sought, and some time near the end of his work in the Congo, he contracted malaria.

The *Guardian*'s obituary called Hamilton "the primary theoretical innovator in modern Darwinian biology, responsible for the shape of the subject today" and *The New York Times* dubbed him "one of the towering figures of modern biology," while *The (London) Independent* reported that Hamilton was "a good candidate for the title of most distinguished Darwinian since Darwin." Hamilton would have been embarrassed by all the attention and saw his life in a very different light. "I grimace," he wrote, "rub two unrequestedly bushy eyebrows together . . . snort through nostrils that each day more resemble the horse-hair bursts of an Edwardian sofa, and, with my knuckles not yet touching the ground, though nearly, galumph onwards to my next paper" (HAMILTON 1996, p. 93).

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