▲ CHAPTER ONE ▲

A Special Difficulty That Might Prove Fatal

While writing *On the Origin of Species* in the late 1850s, Charles Darwin was unencumbered by the strict editorial rules that apply to scientists today. He had the liberty to indulge in wide-ranging digressions that at times became streams of consciousness.[1] This freedom allowed him the scope to tackle issues that he might otherwise have avoided. In particular, Darwin was not afraid to address problems associated with his theory of evolution by natural selection. He did so often, and at length.

This book is about one of Darwin's problems. It began as a small difficulty with honeybees. At first glance, it did not seem like the sort of complication that could sink a theory that many have characterized as the most important one that biology has ever produced. But it turned into a problem that troubled biologists, fascinated naturalists, engaged popular writers and the general public, and even worked its way into political discourse for the next 145 years.

Honeybees had been introduced into Britain around A.D. 45,[2] and by Darwin's day, some five hundred authors had written on bees and beekeeping.[3] By the start of the eighteenth century, England had become the world's leader in the production of apicultural products such as honey and wax, and *The Philosophical Transactions of the Royal Society of London* was an important repository for articles about various aspects of bee life. What's more, the public had fallen in love with bees, particularly when it discovered some of the intriguing natural history of these insects. Bee enthusiasts described how worker bees who were fed "royal jelly" developed into queens and how the same bee egg would develop into a male if it remained unfertilized but become a female if it was fertilized with a drone's sperm.[4]

In practice, what the scientific and public love affair with bees meant was that they could not be ignored in the *Origin*, and as

Darwin biographer Janet Browne notes, Darwin "was specially exorcised over honey bees."[5] If any aspect of bee life was at odds with natural selection, then Darwin understood that it had to be addressed front and center in order for his theory to be credible. One such problem was the existence of nonreproductive—that is, sterile—castes that often occur in insects such as bees, wasps, and ants. These workers are true altruists. In the first place, they do not reproduce but instead provide all sorts of resources to queens—the individuals who *do* reproduce. That alone would make them altruists, in the sense of incurring a personal cost that in turn benefits others. Some, but not all, sterile workers will also defend the hive tirelessly, if need be, with their own lives. This too constitutes an act of altruism, and so the sterile workers who defend the hive are, in a sense, doubly altruistic. And what's more, these bees are designed differently from others in the hive. Differences in size and shape, in fact, allow them to be particularly adept at being altruists.

Sterile social insects were clearly a hurdle for Darwin's theory of natural selection, which posited that only those traits that increased an *individual's* reproductive success would, over subsequent generations, increase in frequency. Sterility and kamikaze-like hive defense would seem to be precisely the sorts of traits that natural selection should operate against, and Darwin knew it.

The process of natural selection, as Darwin saw it, was simple yet extremely powerful: "Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being." For example, Darwin asked his reader to imagine the wolf that "preys on various animals, securing some by craft, some by strength, and some by fleetness." When prey for wolves are scarce, natural selection acts with brute force on wolf populations. "Under such circumstances," Darwin argued, "the swiftest and the slimmest wolves would have the best chance of surviving and so be preserved or selected. . . . I can see no more reason to doubt this, than that man can improve the fleetness of his greyhounds by careful and methodical selection." Wolves possessing the traits that best suit them for hunting survive longer and produce more offspring—offspring, in turn, who possess the very traits that benefited their parents in the first place. Generation

after generation, "slow though the process of selection may be,"[6] noted Darwin, eventually you end up with a wolf better adapted for hunting. There is nothing remotely altruistic going on here: individual wolves do better when they possess certain traits than when they do not, and selection operates to increase the frequency of such traits.

Darwin recognized that natural selection not only operates on morphology (as in the wolf case), but on behavior as well. If behavioral traits were passed from parent to offspring, and these traits had strong, positive effects on longevity and reproductive output, selection would favor such behavioral traits over others. Darwin nicely illustrated how natural selection could operate on behavior by using the egg-laying habits of the cuckoo, a bird notorious for depositing its eggs in the nests of other species. How could such a bizarre trait evolve? What's in it for the cuckoo that such odd behavior should be favored by natural selection?

For Darwin, the potential benefits for parasitic egg-laying behavior abounded. Following his lead, imagine that at the start of this evolutionary process some cuckoos occasionally laid some of their eggs in the nest of another species. Darwin believed that parasitic egg layers might profit "by this occasional habit through being enabled to migrate earlier . . . or if the young were made more vigorous by . . . the mistaken instinct of another species than reared by their own mother." Migrating early and producing more "vigorous" offspring will clearly be favored by the process of natural selection. With such benefits available, if young cuckoos inherited their mother's tendencies to lay eggs in the nests of others, as Darwin thought them "apt" to do, then "the strange instinct of our cuckoo could be, and has been, generated."[7] And again, there is no altruism in play here. As with the wolf case, *if* one variant of a trait—slim, sleek wolf morphology or parasitic egg-laying behavior—is superior to other variants, and if some means exists by which traits are passed from parent to offspring, then natural selection will produce a better-adapted organism.

Evolutionary biologists today recognize that offspring resemble their parents because they inherit their parents' genes. Darwin did not know about genes, nor did he need modern-day genetics for his theory to work. All he needed to realize was that somehow traits that affected reproductive success

were passed from parents to offspring. Any Victorian naturalist worth his salt would have known that offspring resemble their parents, and Darwin was more than a good naturalist, he was a great naturalist.[8]

Since Darwin, of course, Mendel's laws of genetics have become a staple of modern biology, and with the current revolution in molecular genetics, we have a deep understanding of how important genes are in shaping virtually every trait. When it comes to genes and behavior, the modern notion that genes are the fundamental unit passed from generation to generation, and hence the target of natural selection, is often referred to as the "selfish gene" approach—a term first coined by Richard Dawkins in his 1976 book, *The Selfish Gene*.[9] For Dawkins, this approach does not imply that genes are selfish in any emotional or moral sense. In fact, he notes, genes are not anything but a series of tiny bits of DNA put together in a particular sequence and orientation, and somehow distinct from other such tiny bits of DNA. Yet genes can be viewed as "selfish," in that the process of natural selection favors those that can somehow or another get the most copies of themselves into the next generation. In many cases, this will simply come down to a gene's coding for a trait that increases the direct reproductive success of the individual in which it resides. But, as we shall see, this is not the only mechanism by which a gene can get more and more copies of itself into the next generation. There are more indirect, *but equally powerful*, ways for genes to get lots of copies of themselves passed down from one generation to the next.

Natural selection promotes genes that *appear* to be selfish, in the sense of favoring those that maximize the number of copies of themselves that make it to the next generation. Indeed, one of the reasons that Dawkins chose the term "selfish gene" as a metaphor was to emphasize the fact that genes which code for any trait that benefits the species as a whole, or indeed even groups of unrelated individuals, are doomed. Such genes are bound for the evolutionary trash bin because they are not maximizing their chances of being passed to the next generation. Only those genes that are "selfish" make it in the end. Wolf morphology and cuckoo behavior fit nicely into the selfish gene framework; altruism and self-sacrificial hive defense in bees do not, or at least so it appears at first glance.

In the case of Darwin's problem with the bees, he was forced to ask how his theory of natural selection could explain the existence of whole castes of insects that never reproduce and yet protect those that do, even at the cost of their own lives. In other words, what's in it for the altruists? Surely such traits should disappear, and fast, if natural selection worked the way it was supposed to. Altruistic worker bees—whom Darwin recognized as undertaking acts that were "profitable" for others in their hive—appeared to fly directly in the face of his logic.

The existence of sterile altruistic castes was an anomaly that had vexed Darwin since the early 1840s. His worries seem to have stemmed, at least in part, from a reading of Reverend William Kirby and William Spence's textbook *Introduction to Entomology*, in which the authors argued that the incredible behaviors of sterile castes were evidence of the divine hand of the Creator in motion.[10] Darwin's annotations in his own copy of Kirby and Spence's book demonstrate his clear frustration with both the authors' ignorance of basic biology—for example, they implied that neuters could breed—and the whole question of sterile castes and what they meant for his own ideas.[11]

Darwin himself had dabbled in small-scale experiments with social insects at Down House, in one case enlisting the help of his children (William, Henrietta, George, Frank, and Leonard) to better understand various aspects of bee behavior, such as their navigational skills from hive to hive.[12] At one point he had "five or six children each close to a buzzing place," at which point Darwin would tell "the one farthest away to shout out 'here is a bee' as soon as one was buzzing around."[13] Then, like a volunteer fire brigade passing buckets of water down a line, the children along the bee's route would continue signaling until the bees reached Darwin. Though this unconventional use of very young researchers helped Darwin understand communication in social insects, these quasi experiments did little to provide an answer to the mystery of the altruistic castes that permeate the social insects.

It is hard to overemphasize just how concerned Darwin was about the problem of sterile animals that helped others through their acts of altruism. That was simply not the way he envisioned natural selection operating, and at times, the problem of the sterile altruists would, as he himself noted, drive him "half

mad."[14] So frustrated was he, that in the *Origin*, Darwin summarized the whole topic of sterile castes as "one special difficulty, which at first appeared to me to be insuperable, and actually fatal to the whole theory."[15]

Over the course of many years Darwin tinkered with a number of hypotheses that might reconcile the altruistic caste problem—a problem that centered on insects but had implications for any behavior that involved helping others at a cost to self—with his theory of natural selection. In the end, he speculated on how blood kinship might solve the problem of sterile altruistic insects. A hundred years later these ideas would be formalized through an equation that would be called "Hamilton's rule," an equation that would revolutionize the field of evolution and behavior, but the seeds of which were laid in the *Origin*.

In a section of the *Origin* entitled "Objections to the Theory of Natural Selection as Applied to Instincts: Neuter and Sterile Insects," Darwin proposed that the problem of natural selection's producing sterile individuals that often risk their lives to protect others, and appear designed to do just that, ". . . 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."[16] Help your blood kin—your family—and you can make up for any costs that you yourself incur. Take the case of the altruistic bees. Even though individual bee altruists often paid a huge cost both by defending the hive and by not reproducing, this cost was made up by the benefits accrued by their family members, and hence altruistic behavior could, in principle, evolve. In addition to acting as hive guards, in his *Species Book*, Darwin hypothesized that selection might favor such sterile workers, as they also specialize on other tasks, such as foraging.[17] This in turn benefits all family members by relieving them of the task of foraging, and eventually it became very clear to Darwin "how useful their production may have been."[18] Blood kinship and interactions among relatives it turned out, was the key to solving Darwin's problems with both sterility and altruism.

Darwin seems to have realized the importance of the role of blood kinship in explaining altruism as early as 1848. In a manuscript dated June of that year, he hinted at its importance in the context of how some hives with sterile castes may "predominate"

over other hives, presumably as a result of actions that sterile caste members may undertake to help their kin—in Darwin's words, selection would act on "families and not individuals."[19] Help your relatives and you help yourself, albeit indirectly. These ideas, over the course of the next hundred years, would develop into what is today called "kin selection" theory.

The case Darwin presented amounted to this: natural selection could favor the evolution of sterile castes if individuals in such castes helped their blood kin (which they do), because doing so would help ensure the survival of those individuals that could reproduce—individuals with a hereditary makeup very similar to their own. If kin helped each other, even assuming a large cost of so doing (picture the worker honeybee's suicidal attack on nest predators) the process of natural selection could still favor such a trait, because those being helped were similar in their makeup to those doing the helping. In modern-day terms, genes can increase their frequency in the next generation by aiding the reproduction of copies of themselves that just happen to reside in other individuals—blood relatives. Again, Darwin did not know about genes per se, but he did know that blood relatives resembled one another more than strangers, and this was just enough information to speculate on the role of kinship in the evolution of altruism.

Darwin was still somewhat ambivalent about the power of this explanation in 1848,[20] but over the next decade he became more and more convinced of the utility of his initial explanation—so much so that it found its way into the *Origin*, when so many of Darwin's early arguments did not. One turning point in his thinking on the power of blood kinship in evolution took place when he read William Youatt's work on cattle breeding.[21] As Darwin noted, cattle breeders are interested in producing meat with the "flesh and fat to be well marbled" together. The problem is that to get such meat, a breeder must kill the cattle that produce it. Developing breeding lines of cattle, then, with just the right mixture of flesh and fat marbled together would seem impossible using standard techniques that involve breeding individuals with the desired trait, since in this case, such individuals are slaughtered for their meat. Darwin notes that to solve this problem "the breeder goes with confidence to the same family and has succeeded."[22] In other words,

even in the pregenetic era, breeders were aware that blood kin were very likely to resemble one another, and so to achieve a desired trait—in this case, marbled meat—one could breed from blood relatives.

The second intellectual pillar for Darwin's thoughts on kinship and the evolution of altruism derived from his discussions about social insects with his entomologist colleague, Fredrick Smith. As Darwin ultimately saw the situation, "this principle of selection, namely not of the individual which cannot breed, but of the family which produced such individuals, has I believe been followed by nature in regard to the neuters amongst social insects."[23] In some instances, he referred to this as selection at the level of the community (the hive, for example) rather than the kin group per se. Indeed, as Robert Richards details in his book *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*, Darwin discussed such "community-level" selection in a number of instances.[24] But when it came to altruism and the social insects, the communities to which Darwin referred in the *Origin* were almost always made up of blood relatives. That said, some of Darwin's intellectual descendants would return to community-level selection in their own quests to understand the evolution of altruism.

In one sense, by turning to kinship for the answer, Darwin both posed and solved the conundrum of the evolution of altruism. The problem was confronted, as in the case of sterile insects, and the remedy—what we would now call kin selection—was proposed. But in two very important ways that would haunt the field for a century after the *Origin*, Darwin failed to settle the issue. First, without experiments or some sort of mathematical framework for his theory, he was never able to answer the questions his theory brought forth, namely: precisely how does what we now call kin selection operate? For example, just how does the *degree* of kinship affect the evolution of altruism? Some blood kin, such as parents and offspring or siblings, are very closely related, but other sets of relatives, like second cousins, are much less so. Does that matter, and if so, exactly what does it mean in terms of the predictions one can make regarding the evolution of altruism? Further, does it matter how costly the altruistic act or how large a benefit to the donor of such altruism? If so, how are these costs and benefits

to be measured, and what's more, how does ecology affect such costs and benefits?

These fundamental questions required answers. Indeed, in the long run, they would require a mathematical model of kinship and altruism—a model that made specific and testable predictions. Without this, Darwin's ideas on kinship and altruism were akin to a verbal precursor to Einstein's mathematical theory of relativity: nice, but lacking in the hard equations that are needed to establish a bedrock theory. It would take a good hundred years for such models of kin selection theory to appear on the scene.

The second, and in some ways just as important, question that Darwin opened up for debate was one that he never got into, but one that would forever intertwine itself in all future discussions of blood kinship and altruism. And this question—do evolutionary pressures to be kind and generous to others extend beyond blood relatives?—has implications for a much broader audience. From an evolutionary perspective, to what extent do we expect to see generosity as a family affair, and only a family affair?

Consider this: Public outrage follows a judge's order that a child be taken from foster or adoptive parents—maybe the only mother and father the child has ever known—and delivered back to the child's biological parents. But in most such situations, the judge has little choice. Our legal system recognizes blood kinship as a special relationship that society has an obligation to protect, absent some severe aberration in the biological parents that renders them incapable of raising their own child. Of course, just because an idea is codified into law, does not mean that it is scientifically valid. The point here is different: namely, the notion that altruism is particularly pronounced between blood kin is so universally held that it has worked its way into our very legal system. Darwin was silent on such issues. But what started as a scientific matter about social insect evolution ends up having much broader implications.

Those broader implications were understood in Darwin's day as well as our own. For one thing, by directly addressing the problem of honeybee altruism, Darwin not only tackled a major obstacle that stood in the path of his scientific theory, he also further alienated some religious individuals who were already struggling with his idea that natural processes could explain the

diversity of life that we see around us. For when it came to altruism, kinship, and social insects, Darwin was not using his theory to suggest how we get a new species of barnacle or earthworm. Rather, he was positing a hypothesis for how self-sacrificial behavior—a subject which, to that moment in time, had been reserved for religion to address—could come into existence. And to make the situation even more complicated, Darwin's ideas clearly meant that altruism could (and did) evolve in creatures other than humans, and that by studying such creatures we could potentially better understand our tendency to be altruistic, particularly toward blood kin.

And not only religious individuals were troubled by what Darwin was saying about kinship and altruism, nor is this surprising. Darwin was on fairly safe ground when discussing complex anatomical structures like the insect eye, because this was not something that the lay public necessarily understands or even cares to understand. But altruism is not like the insect eye. Very few people have their own theories about how the insect eye evolves, but almost everyone has his or her own ideas on why humans are or are not altruistic. These ideas are often spawned from philosophy, religion, and politics, but sometimes arise solely from gut feelings about why we are the way we are. And, of course, scientists too have their philosophical, religious, and political views, and they are not immune from the influence of such ideas on their scientific work; particularly when the questions being studied have, by their very nature, implications for philosophy, religion, and politics.

Over and over we shall see how personal views weave their way into the hundred-year odyssey from Darwin's original ideas to our modern mathematical models of altruism and kinship. Scientists can certainly construct very objective experiments on kinship and altruism, even if they have personal opinions on the subject; it is just more difficult to do so than it is for other topics, because it has such broad implications about the foundations of goodness. And everyone cares about that. Many of the scientists we will encounter seemed almost obsessed with understanding the role that kinship plays in the evolution of altruism—much more so than we see when people study the evolution of almost any other trait. The reason is simple. Unraveling how blood kinship affects altruism would not only be hailed as a major scientific

achievement (and it was), but it would tell us so much about our very nature.

Given the central role that the desire to understand goodness—or its absence—holds in human psyche, it is hardly surprising that not long after Darwin published *On the Origin of Species*, the questions surrounding kinship and the evolution of altruism got personal. In 1888, a long-standing argument over kinship and altruism intensified between two of the best-known personalities of their time: Thomas Henry Huxley, "Darwin's bulldog," and Petr Kropotkin, an anarchist former prince of Russia, who would pen a classic book on evolution and kinship entitled *Mutual Aid*. Huxley took his old friend Darwin's ideas to a logical extreme, contending that altruism was rare, but that when it occurred, it was *always* tied to blood kinship. Kropotkin saw things in a radically different way. Altruism (what he called "mutual aid") could be observed everywhere in the world, and Kropotkin was certain it had nothing to with kinship. His fight with Kropotkin would make Huxley better understand Darwin's lament, "I often think my friends (and you far beyond others) have good cause to hate me, for having stirred up so much mud and led them into so odious trouble."[25]