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CHAPTER I

Liar, Liar, Everywhere

She is pregnant. Raising a child takes a lot of time and energy, yet she is short of both. Homeless, she has no choice but to find somebody else to take care of her baby—for free. It's not easy, but she knows how to pull it off. She scouts around and spots a cozy house in a quiet neighborhood. The young wife of the family looks caring and has just given birth to a new baby, so is a perfect choice as a surrogate. She hides herself and waits in the vicinity, keeping watch on the house. Opportunity presents itself when the new mother takes a short trip to get some food. She sneaks in and switches the baby with her own. Then she heartlessly throws the victim's infant in a dump.

What you have just read is a cold-blooded murder case, one that takes place in nature when a female cuckoo bird sneaks her egg into a warbler's nest. The cuckoo is cheating, though the scenario doesn't quite fit *Oxford English Dictionary*'s definition of the verb "cheat": to "act dishonestly or unfairly in order to gain an advantage." Cheating in humans usually involves an element of intention. In the larger biological world, however, establishing intent is neither easy nor necessary. For biologists, as long as organisms act to favor themselves at the expense of others—especially in situations when cooperation is expected—they are cheating.[1]

This book is about the behavior, evolution, and natural history of cheating. Although, in common usage, the word "cheating" is often interchangeable with "lying" and "deceiving," the three words differ in connotation, nonetheless. Furthermore, lying and deceiving involve two very different biological processes, as we will unveil in the next two chapters. In light of this new insight, the word "cheating" refers to both lying and deceiving in the book.[2]

Cheaters are everywhere in the biological world, according to our broadened definition of cheating. Monkeys sneak around for sex; possums, well, play "possum," as they are famous for when pursued by a predator; birds scare rivals away from contested food by crying wolf—emitting alarm calls that are normally used to warn others about an approaching predator; amphibians and reptiles are master impostors, altering their body color to blend into their backgrounds; stickleback fish protect their eggs and babies by misdirecting their cannibal peers away from their nests; defenseless caterpillars ward off predators by masquerading as dangerous animals such as snakes with big false eyes (see color plate 1); squids escape from predators by ejecting ink to create a "smoke screen" in the water. Examples of lying and deceiving behavior in animals can go on and on.

What may surprise you is that cheating doesn't require a brain, or even a neuron, as many plants are cheaters as well. For example, most orchids mimic the aromas of their pollinators' food. Around 400 orchid species, however, evolved a more audacious tactic: they fool male pollinators by mimicking the smell and appearance of female insects to take advantage of eager males who seek opportunities to mate (see color plate 2). Even more amazing, these plants can keep male pollinators aroused by preventing them from ejaculating. Thus, the unsatisfied male pollinators will keep going in search of another female—including a female-apparent flower—to mate with. Since these males are highly promiscuous, they are extremely effective in spreading orchid pollen.[3]

Fungi cheat too. For example, truffles—mushroom-like species that form fruiting bodies underground—emit a steroid called androstenol that mimics the pheromone of wild boars. Androstenol is produced in the testes of adult boars and has a musty odor to the human nose. When female pigs sense the truffle aroma, they will dig exuberantly for the source. What they don't know is that they are being suckered by something bearing no resemblance to the swine beau they are hoping for. The only outcome of their passionate fervor is spreading spores for the truffles.[4] Mission accomplished for the fungi that deceive.[5]

Complex organisms such as plants and fungi cheat; so does single-celled life. A good example is the slime mold (or social amoeba) known by its scientific name, *Dictyostelium discoideum* (or "Dicty" for short). When starved, the slime mold amoeba cells gather together to form a mobile, slug-like structure. The "slug" moves as a unit until it finds a suitable spot and then grows into a fruiting body made of a spore-producing head mounted on a thin stalk. The entire thing is shaped like a lollipop or a maraca (a rattle-like percussion instrument popular in Latin America) (fig. 1.1). The cells in the head, which consists of 80% of all cells, will seed the next generation when food becomes plentiful again. The other 20% of the cells consigned to the stalk, however, rot away after completing their mission—to raise the head so that the spores can scatter far and wide, like dandelions spreading their fluffy seeds in the wind.

If you were a slime cell, where would you prefer to end up—the head or the stalk of the fruiting body? The head, of course! Because only in the head do you have the opportunity to pass your genes to the next generation. If you were a cell in the stalk, your genes would be destined for an evolutionary dead end. Who, in the biological world, wants to be relegated to an inferior status, without a chance to reproduce?

Fortunately, this isn't a major issue when amoeba cells have the same genetic makeup, like identical twins. When cells share an identical set of genes, it matters little as to which cells seed the next generation. However, when a fruiting body is made of a chimera of two or more types of cells, where many of the genes are different, conflict ensues. They all compete to be part of the fertile head rather than play a supporting role in the sterile stalk. As one might expect, different cells play dirty in order to make it into the prized head by any means necessary, including cheating.[6] Some types of cells, enabled by certain genetic mutations, defraud others by sending more than their fair share of "representatives" to the head,[7] a maneuver similar to political gerrymandering. Moreover, once they have made it to the head, they produce noxious chemicals to

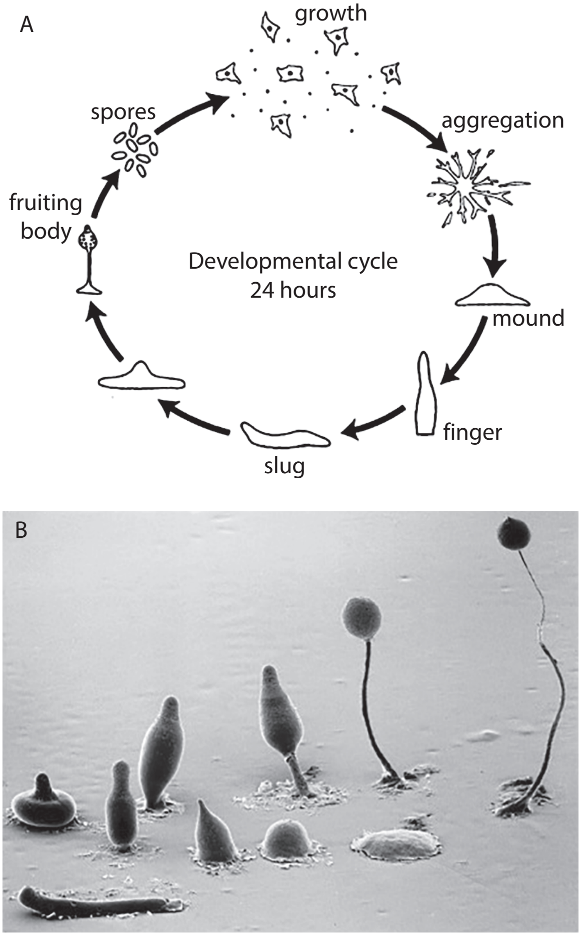

FIGURE 1.1. The developmental cycle (A) and sequence of spore formation (B) in the social slime mold *Dictyostelium discoideum* (Myre 2012).

prevent latecomers from getting into the lifeboat for the next generation. Recent studies have revealed that more than 100 mutant genes are implicated in this amoeba cheating scam.[8]

Next, let's visit the bacterial world to see whether they also cheat. Bacteria are tiny. Individuals alone can't do much. Just as building the Great Wall involved hundreds of thousands of humans, achieving collective bacterial tasks (such as emitting light—bioluminescence—and trapping vital elements from the environment) requires millions of bacteria working together toward a common goal. That's why bacteria often congregate to form a thin, slimy layer called biofilm in soil or water.

Among their communal projects is gathering iron, an element critical for bacteria to survive. The problem they face is that iron is usually found in low concentrations in their surroundings. Because individual bacteria can't do much on their own, collecting iron is necessarily a collaborative work for the community. To coordinate their efforts, bacterial members "talk" with one another by releasing chemicals that signal particular genes to "turn on" in sync to make a family of complex compounds called siderophores. Siderophores are related to hemoglobin in our blood cells in that they can bind with iron. In this way, they serve as bacteria's fishing net to scoop up iron floating in the environment.

But there is a catch. Siderophores are costly to produce for individual bacteria in terms of material and energy. Yet they are a public good, a "commons" shared by all members in the community. As we all know, once you have a public good, there are often cheaters who come along for a free ride. Who hasn't been in a situation where some team members take credit for the group's work yet contribute less than other members?

Bacteria also suffer from this social dilemma. There is no shortage of free riders that contribute less than their fair share to the production of siderophores yet still devour the catch—iron—along with all the others who've done the work.[9] Obviously, cheaters can sabotage the collective effort. If they are too numerous, productivity of siderophores will drop, and the amount of iron collected will decline, which in turn will put the livelihood of the entire community at risk. Threatened by this potentially fatal consequence, honest producers have evolved an arsenal of antifraud strategies. Some bacteria, for example, can band together with their genetic look-alikes to prevent free riders from infiltrating their community. They may even use toxins to kill the cheaters.[10]

Even viruses cheat. Viruses are not considered fully alive, because they lack the necessary biological tools to survive and reproduce on their own. They have to steal their hosts' resources and genetic machinery to complete their life cycles. This means that to engage in cheating does not require a complete form of life.

Blatant cases of viral cheating have been well-documented. One example occurs when different viral species or different variants of the same species infect a single host cell. Their biological resources—such as genes and proteins—can become mixed. This provides opportunities for some viruses to use trickeries to steal the resources produced by others that serve as unwilling helpers. In this way, cheating viruses don't need to possess all the genes essential for making copies of themselves or for assembling their protein coatings, known as capsids, that package their genetic material within.[11]

What we have seen so far are cases of cheating between different individuals, simple or complex, unicellular or multicellular. Cheating can also take place within the same individual. Cancer cells, for example, are cheating cells that shirk the duty of cooperation with other cells in the body. They instead gobble up all the resources, proliferate, and refuse to commit suicide when commanded to do so. Thus, fighting cancer is essentially fighting cheating cells, a point made clear in Athena Aktipis's 2020 book, *The Cheating Cell*.

Even inside a typical cell, cheating is part of life. For instance, the B chromosome ekes out a living by cheating. In sharp contrast to the normal "A" chromosomes that are familiar to us, B chromosomes are smaller and can be common, and they can be found in varying numbers within a cell (fig. 1.2). What makes them stand out is their ability to tag along without doing any work. In other words, they are passed on, generation after generation, by hitchhiking without contributing to cell functionality, akin to party crashers living on free food while enjoying themselves at their host's expense.

Even genes cheat. Your body is a vessel for a vast amount of genetic garbage known as junk DNA. Just like B chromosomes, junk DNA serves no purpose for its host organism but gets a free ride from generation to generation.[12] The amount of junk DNA is truly awe-inspiring. It accounts for up to 98% of our genome, encompassing many varieties of useless genetic material, such as repeated elements, pseudogenes, and transposable elements (the last of which are more vividly called jumping genes).

FIGURE 1.2. B chromosomes (marked with "B") in the roe deer (modified from Graphodatsky et al. 2011).

Jumping genes are fragments of DNA that can insert themselves almost anywhere in the genome through a copy-and-paste process, much as we do in a word processing program. They are so prolific that they make up 45% of the entire human genome.[13] A well-known jumping gene is the *Alu* element. With a length of about 300 base pairs, the *Alu* element has multiplied more than a million copies of itself in the evolutionary lineage leading to humans over the last 53 million years. Today, it makes up 10.7% of the entire human genome.[14] Because of the hyperactive nature of jumping genes and their ability to promote themselves, the genome of salamanders can be 40 times larger than that of humans.[15] Since all animals (in fact, all eukaryotic organisms) have roughly the same number of working genes, what salamanders can boast about is an extremely large genetic junkyard.

As befits their name, jumping genes jump, and they jump randomly in the genome. Because the vast majority of our DNA is junk, whenever a jumping gene replicates itself and places the copy in a new location in our genome, it usually has no noticeable effect, like adding a new bag of trash in a huge landfill. But once in a while such an insertion may hit an area in the middle of a functional gene. If this happens, it can result in a serious genetic defect and lead to health problems such as cancer or hemophilia.[16]

Intrigued by jumping genes? There are also bizarre cases of cheating genes called selfish genetic elements or, more colorfully, outlaw genes. Among the most famous are genes known as segregation distorters or meiotic drivers in insects. In the common lab fruit fly, *Drosophila melanogaster*, these genes can boost their own representation in the genome by killing sperm cells that carry alternative alleles. In doing so, these outlaw genes get more than their fair share of what would normally be an even split.[17] If these outlaw genes are located on the X or Y chromosome, it may result in a lopsided sex ratio (more males or females), rather than a 50:50 divide.[18]

The last case of cheating genes I want to describe are known as converting elements. These genes code for enzymes called homing endonucleases, which can cut open a DNA chain at specific locations. They then add a replica of themselves into the breach.[19] It's like a rogue physician who uses his own sperm to inseminate eggs from women who come to him seeking artificial fertilization.

Converting elements commit a genetic fraud by violating the rules followed by other genes. The genes that play by the rules may be hurt directly by becoming disabled, or indirectly by being outcompeted in an unfair race. Like jumping genes, converting elements can be transmitted horizontally, copying and inserting themselves into the genome of their peers in addition to their own descendants. (Unexpectedly, this "rogue" quality of self-promotion has given a new halo to homing endonucleases today: it's the foundation for the technology of gene editing called CRISPR, pioneered by Jennifer Doudna and Emmanuelle Charpentier, who together won the 2020 Nobel Prize in Chemistry.)

Selfish genetic elements such as B chromosomes, jumping genes, segregation distorters, and converting elements share a common feature: they all promote their own interests at the expense of other genes. Since the transmission patterns of these genetic elements violate classical Mendelian laws, you may feel that you learned the wrong things in high school biology class. But no worry. Biological systems are complex and are rarely governed by universal laws as in physics. Because of this, biology is known for being a science of exceptions.

The above section, although citing only a few examples, demonstrates that cheating is found in all domains of life, at every level of the biological hierarchy, from the most complex organisms to the least sophisticated, even incomplete, forms of life. It is found among animals, plants, fungi, bacteria, viruses, chromosomes, genes, and snippets of

DNA. It occurs within the same individual, between individuals of the same species, and between species that are vastly different in form and function.

Regardless of their prevalence in nature, however, the words cheating, lying, and deception all come with negative connotations due to our moral preference and the premium we place on honesty. Although we value truth and loathe lies, real life often runs counter to what we ideally want. Contrary to the long-held dictum, honesty is not always the best policy in our daily lives.

Consider this case. An innocent man has been falsely charged, convicted, and condemned to die. Desperate to save him, his loyal friends propose a way out: escape by bribing the jailer. Even when faced with this choice, however, he declines on the ground that to do so would be cheating the legal system. What do you think about the concept of honesty as applied by this man? If you were in his position, what would you do?

If you think the man's choice is foolish, congratulations! You've just saved the life of Socrates, the Greek philosopher who chose death over breaching the trust between a citizen and the state. How likely is it that we would find a heroic martyr, willing to die for the sake of trust and honesty, in the natural world? Extremely unlikely—in fact, no known examples exist. On the contrary, we find that cheating is ubiquitous in nature at all levels.

Why is cheating so common in the biological world? The answer: evolution is not a Socratic philosopher. It is, instead, an unmoral, heartless process that proceeds pragmatically without any concern over ethical preferences, honor codes, or value systems. It certainly makes no distinction between prosocial cooperation and antisocial manipulation, because all that matters is what works to enhance survival and reproduction. Any trait—be it morphological, physiological, behavioral, or genetic—can prevail as long as it can boost its owner's Darwinian fitness, defined and measured as the number of offspring born and raised to adulthood. Furthermore, while freeing cheating from our moral consideration, evolution punishes those who forgo it as a strategic option when using it can increase their fitness. As a result, even though it might seem brazen and despicable to our human social sensibilities, cheating thrives in the biological world.

So, cheating flourishes in nature as a direct result of natural selection. Less well-known, however, is that cheating also serves as a potent selective force that drives evolution on its own. The reason is simple in concept: cheating favors the cheater and hurts the cheated. As such, it spurs the emergence of counter-cheating tactics, which in turn beget counter-counter-cheating strategies, ad infinitum. And during this ongoing evolutionary arms race, to quote Darwin, "endless forms most beautiful and most wonderful have been, and are being, evolved."

To illustrate this point, take cheating in rhizobia, soil bacteria that live in the roots of plants—specifically legumes. These bacteria fix nitrogen for plants, whereas the plants provide housing facilities and food in the form of carbon. So, the relationship is supposed to be happily mutualistic—or so we traditionally thought. But a close examination has revealed that, rather than a love affair, the relationship between rhizobia and their plant hosts is far more complicated. Some rhizobia actually produce very little nitrogen. That is, they cheat in order to get free housing and carbon from the plants.[20] For this reason, not all plants welcome rhizobia. Some are known to fight back by cutting off the nutrient supply if cheating rhizobia are too numerous. Only those living in poor soil, desperately in need of nitrogen, would grudgingly put up with an unfair relationship with rhizobia.[21] Apparently, beggars can't be choosers. This demonstrates how cheating can unleash a cascade of new moves and countermoves as the bacteria and their hosts try to get the upper hand in their relationship.

Intrigued by the complex strategies emerging from the evolutionary game played by rhizobia and plants? This is just a simple case to illustrate how cheating can trigger an evolutionary arms race and become a powerful catalyst for the creation of diversity, complexity, and even beauty, as we will see in the following chapters.

Unfortunately, the role of cheating in evolution remains underappreciated today for two key reasons. One is historical. Darwin himself did not address cheating as a major force in evolution by natural selection. *On the Origin of Species* never mentions the word "cheat" but uses the word "deceive" seven times. Only three are related to animal cheating—all are forms of mimicry, protective disguises employed by tasty bugs to fool their predators. Clearly, how cheating relates to evolution and biodiversity wasn't on his mind—at least not high in priority among his many ideas.

Darwin's omission implies the second reason for us to overlook the importance of cheating. It's easy to see natural selection in terms of unrelenting, cutthroat competition for resources between rivals, or in terms of surviving the onslaughts of predators, parasites, and pathogens. Because of this, evolution has been popularly stereotyped as "survival of the fittest" and "nature red in tooth and claw." Such a one-dimensional impression tends to divert our attention from the soft power of cooperative behaviors that are fully as effective for enhancing fitness in numerous situations and contexts, a point made clear by many scientists during recent decades.

In some animals, social intelligence is significantly more important than physical strength. In a bonobo group, for instance, success in terms of fitness is predicated on the strength of an individual's social network. A brawny brute who relies on sheer individual muscle power is destined to be a loser when faced with the united efforts of cooperating members of the group. Without some needed social intelligence, he could also become an object of manipulation, exploited by others. This is why cheating, a catalyst for social intelligence, matters so much in evolution.

With the emergence of modern human intelligence, the arms race between cheating and counter-cheating strategies was not only vastly expanded and intensified but also began to take place at a whole new level—the arena of cultural evolution. And just as it results in the emergence of novel biological traits, cheating is a potent catalytic force that spurs many cultural innovations, which then lead to cultural diversity and complexity. Without cheating, there would be no literature, art, science, technology, business, or religion—and the list goes on until it encompasses all aspects of our lives, society, and culture. This may seem deeply counterintuitive for now, but the reasons will become evident later when we zero in on how modern technologies and cultural institutions evolve and transform in sync with cheating.

Despite my emphasis on the catalytic power of cheating, I have no desire or intent to create a revisionist account of the virtue of lies. On the contrary, many forms of cheating, whether or not they are considered criminal offenses, can cause substantial harm to innocent people. That's why no serious moral philosophy or religion would endorse or advocate cheating. As social scientists have amply shown us, the basic cultural glue that binds us together as a human society is trust.[22] Though it may not seem so from what I've portrayed in this chapter, this book will reinforce this point from a biological perspective. It's unthinkable that a society could sustain itself for long without honesty and truth as its moral foundations. That's why we humans have fought so hard to suppress cheating and cheaters for millennia.

Yet, despite our best efforts, cheating has been a persistent and perennial problem in all known human societies across history. No society, in fact, has ever succeeded in completely wiping it out. Moreover, as if the problem were not bad enough, cheating has become perceptibly worse in the Information Age. Not only do all traditional trickeries continue to exist, but cheating has extended itself into the digital realm, where it has found a fertile environment to thrive. A vast number of new scams, from phishing to sextortion, are emerging and evolving with increasing sophistication and reach. At the societal level, the ubiquity of fake news and conspiracy theories poses a major threat to democracy. By preventing citizens from acquiring accurate and reliable information, it undermines our ability to agree on the basic nature of truth and fact.[23] What should we do about cheating, given that we are unable to root it out?

The seemingly quixotic and fatalistic campaign against cheating doesn't mean that it's not worth trying, nor that we're doomed to lose. Rather, it gives us an opportunity to rethink our approach in this digital age and find new ways to deal with a problem that has been with us since time immemorial. In this respect, evolutionary science can offer a trove of wisdom for us to tap into.

This book will provide a tour into the world of cheaters to see how organisms use a broad spectrum of methods to deceive, hustle, and swindle others for their own gain. More importantly, we'll search for the modus operandi behind the vast diversity of tricks, scams, and frauds. We will then use our newly acquired evolutionary understanding of how cheaters operate to design novel strategies to combat cheating in our society.

Specifically, we will, in the next two chapters, journey into how animals cheat by using two rules that carry through the book. We will then find reasons for how and why honesty can survive and flourish amid the onslaught of lies and deceptions in chapter 4. With this information in mind, we will turn to chapter 5 to see how cheating can spur the emergence of novel features including behavior, intelligence, and art, all through evolutionary arms races. This will be followed by two chapters about human cheating and self-deception, respectively, showing that the rules used in cheating apply in both the biological realm and human cultures. Finally, we will venture into philosophical terra incognita, attempting to settle the age-old controversy: Is there any cheating that is morally acceptable?

When you close the book, I hope you'll be convinced by the book's main premise and overarching goal: cheating is a powerful catalyst that contributes to the creation of diversity, complexity, and beauty in the biological and cultural world. By understanding how it works, cheating can be practically contained, even though it may seem like an inevitable and invincible part of life.

Now, buckle up for a thrilling journey into the world of cheating.

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