

*Ten*

## The Evolution of Behavior

**A**t last we reach the foundations. Genes and promoters evolve. As do transcription factors, transposases, and splicing enzymes. As has every trait touched by genetic influences (i.e., everything). In the words of the geneticist Theodosius Dobzhansky, “Nothing in biology makes sense except in the light of evolution.” Including this book.<sup>[1](#)</sup>

## EVOLUTION 101

**E**volution rests on three steps: (a) certain biological traits are inherited by genetic means; (b) mutations and gene recombination produce variation in those traits; (c) some of those variants confer more “fitness” than others. Given those conditions, over time the frequency of more “fit” gene variants increases in a population.

We start by trashing some common misconceptions.

First, that evolution favors *survival* of the fittest. Instead evolution is about reproduction, passing on copies of genes. An organism living centuries but not reproducing is evolutionarily invisible.\* The difference between survival and reproduction is shown with “antagonistic pleiotropy,” referring to traits that increase reproductive fitness early in life yet decrease life span. For example, primates’ prostates have high metabolic rates, enhancing sperm motility. Upside: enhanced fertility; downside: increased risk of prostate cancer. Antagonistic pleiotropy occurs dramatically in salmon, who epically journey to their spawning grounds to reproduce and then die. If evolution were about survival rather than passing on copies of genes, there’d be no antagonistic pleiotropy.<sup>2</sup>

Another misconception is that evolution can select for preadaptations—neutral traits that prove useful in the future. This doesn’t happen; selection is for traits pertinent to the present. Related to this is the misconception that living species are somehow better adapted than extinct species. Instead, the latter were just as well adapted, until environmental conditions changed sufficiently to do them in; the same awaits us. Finally, there’s the misconception that evolution directionally selects for greater complexity. Yes, if once there were only single-celled organisms and there are multicellular ones now, average complexity has increased. Nonetheless, evolution doesn’t necessarily select for greater complexity—just consider bacteria decimating humans with some plague.

The final misconception is that evolution is “just a theory.” I will boldly assume that readers who have gotten this far believe in evolution. Opponents inevitably bring up that irritating canard that evolution is unproven, because (following an unuseful convention in the field) it is a “theory” (like, say, germ theory). Evidence for the reality of evolution includes:

- Numerous examples where changing selective pressures have changed gene frequencies in populations within generations (e.g., bacteria evolving antibiotic resistance). Moreover, there are also examples (mostly insects, given their short generation times) of a species in the process of splitting into two.
- Voluminous fossil evidence of intermediate forms in numerous taxonomic lineages.
- Molecular evidence. We share ~98 percent of our genes with the other apes, ~96 percent with monkeys, ~75 percent with dogs, ~20 percent with fruit flies. This indicates that our last common ancestor with other apes lived more recently than our last common ancestor with monkeys, and so on.
- Geographic evidence. To use Richard Dawkins's suggestion for dealing with a fundamentalist insisting that all species emerged in their current forms from Noah's ark—how come all thirty-seven species of lemurs that made landfall on Mt. Ararat in the Armenian highlands hiked over to Madagascar, none dying and leaving fossils in transit?
- Unintelligent design—oddities explained only by evolution. Why do whales and dolphins have vestigial leg bones? Because they descend from a four-legged terrestrial mammal. Why should we have arrector pili muscles in our skin that produce thoroughly useless gooseflesh? Because of our recent speciation from other apes whose arrector pili muscles were attached to hair, and whose hair stands up during emotional arousal.

Enough. Don't get me started.

---

Evolution sculpts the traits of an organism in two broad ways. “Sexual selection” selects for traits that attract members of the opposite sex, “natural selection” for traits that enhance the passing on of copies of genes through any other route—e.g., good health, foraging skills, predator avoidance.

The two processes can work in opposition.<sup>3</sup> For example, among wild sheep one gene influences the size of horns in males. One variant produces large horns, improving social dominance, a plus for sexual selection. The other produces small horns, which are metabolically cheaper, allowing males to live and mate

(albeit at low rates) longer. Which wins—transient but major reproductive success, or persistent but minor success? An intermediate form.\* Or consider male peacocks paying a price, in terms of natural selection, for their garish plumage—it costs a fortune metabolically to grow, restricts mobility, and is conspicuous to predators. But it sure boosts fitness via sexual selection.

Importantly, neither type of selection necessarily selects for “the” most adaptive version of a trait, which replaces all others. There can be frequency-dependent selection, where the rarer version of two traits is preferable, or balanced selection, where multiple versions of traits are maintained in equilibrium.

## BEHAVIOR CAN BE SHAPED BY EVOLUTION

Organisms are amazingly well adapted. A desert rodent has kidneys that excel at retaining water; a giraffe's huge heart can pump blood up to its brain; elephants' leg bones are strong enough to support an elephant. Well, yes—it *has* to work that way: desert rodents whose kidneys weren't great at retaining water didn't pass on copies of their genes. Thus there is a logic to evolution, where natural selection sculpts traits into adaptiveness.

Importantly, natural selection works not only on anatomy and physiology but on behavior as well—in other words, behavior evolves, can be optimized by selection into being adaptive.

Various branches of biology focus on the evolution of behavior. Probably best known is sociobiology, premised on social behavior being sculpted by evolution to be optimized, just as biomechanical optimization sculpts the size of a giraffe's heart.<sup>4</sup> Sociobiology emerged in the 1970s, eventually generating the offshoot evolutionary psychology—the study of the evolutionary optimization of psychological traits; as we'll see, both have been plenty controversial. As a simplifying convenience, I'll refer to people who study the evolution of social behavior as “sociobiologists.”

## THE DEMISE OF GROUP SELECTION

We start by grappling with an entrenched misconception about the evolution of behavior. This is because Americans were taught about the subject in the 1960s by Marlin Perkins on the TV program *Mutual of Omaha's Wild Kingdom*.

It was great. Perkins would host. Jim, his sidekick, did dangerous things with snakes. And there were always seamless segues from the program to ads from Mutual of Omaha—"Just as lions mate for hours, you'll want fire insurance for your home."

Unfortunately, Perkins espoused wildly wrong evolutionary thinking. Here's how it looked on the program: It's dawn on the savanna; there's a herd of wildebeest on a river's edge. The grass is greener on the other side, and everyone wants some, but the river teems with predatory crocodiles. The wildebeest are hemming and hawing in agitation when suddenly an elderly wildebeest pushes to the front, says, "I sacrifice myself for you, my children," and leaps in. And while the crocs are busy with him, the other wildebeest cross the river.

Why would the old wildebeest do that? Marlin Perkins would answer with patrician authority: because animals behave For the Good of the Species.

Yes, behavior evolves by "group selection" for the good of the species. This idea was championed in the early 1960s by V. C. Wynne-Edwards, whose wrongness made him modern evolutionary biology's Lamarck.\*<sup>5</sup>

Animals don't behave for the good of the species. But what about that wildebeest? Look closely and you'll see what really happens. Why did he wind up saving the day? Because he was old and weak. "Good of the species" my keister. They pushed the old guy in.

Group selection was done in by theoretical and empirical studies showing patterns of behavior incompatible with it. Key work was done by two gods of evolutionary biology, George Williams of SUNY Stony Brook and Oxford's Bill ("W.D.") Hamilton.<sup>6</sup> Consider "eusocial insects," where most individuals are nonreproductive workers. Why forgo reproduction to aid the queen? Group selection, obviously. Hamilton showed that eusocial insects' unique genetic system makes a colony of ants, bees, or termites a single superorganism; asking

why worker ants forgo reproduction is like asking why your nose cells forgo reproduction. In other words, eusocial insects constitute a unique type of “group.” Williams then elaborated on how the more standard genetic system, in species from noneusocial insects to us, was incompatible with group selection. Animals don’t behave for the good of the species. They behave to maximize the number of copies of their genes passed into the next generation.\*

This is the cornerstone of sociobiology and was summarized in Dawkins’s famed sound bite that evolution is about “selfish genes.” Time to see its building blocks.

## INDIVIDUAL SELECTION

Passing on lots of copies of one's genes is accomplished most directly by maximizing reproduction. This is summarized by the aphorism "A chicken is an egg's way of making another egg"—behavior is just an epiphenomenon, a means of getting copies of genes into the next generation.

Individual selection fares better than group selection in explaining basic behaviors. A hyena bears down on some zebras. What would the nearest one do if she's a group selectionist? Stand there, sacrificing herself for the group. In contrast, an individual selectionist zebra would run like hell. Zebras run like hell. Or consider hyenas that have just killed a zebra. Group selection mind-set—everyone calmly takes turns eating. Individual selection—frenzied free-for-all. Which is what occurs.

But wait, says the group selectionist, wouldn't the zebra species benefit if it is the fastest animals who survive and pass on those fast-running genes? Ditto for the group benefits of the fiercest hyena getting the most food.

As more nuances of behavior are observed, clinging to group selection requires increasingly tortuous arguments. But one single observation devastates group selection.

In 1977 the Harvard primatologist Sarah Blaffer Hrdy documented something remarkable—langur monkeys in the Mount Abu region of India kill one another.<sup>7</sup> People already knew that some male primates kill one another, fighting for dominance—okay, makes sense, boys will be boys. But that's not what Hrdy reported; male langurs were killing infants.

Once people believed her careful documentation, there was an easy answer—since babies are cute and inhibit aggression, something pathological must be happening.<sup>8</sup> Maybe the Abu langur population density was too high and everyone was starving, or male aggression was overflowing, or infanticidal males were zombies. Something certifiably abnormal.

Hrdy eliminated these explanations and showed a telling pattern to the infanticide. Female langurs live in groups with a single resident breeding male. Elsewhere are all-male groups that intermittently drive out the resident male; after infighting, one male then drives out the rest. Here's his new domain,



consisting of females with the babies of the previous male. And crucially, the average tenure of a breeding male (about twenty-seven months) is shorter than the average interbirth interval. No females are ovulating, because they're nursing infants; thus this new stud will be booted out himself before any females wean their kids and resume ovulating. All for nothing, none of his genes passed on.

What, logically, should he do? Kill the infants. This decreases the reproductive success of the previous male and, thanks to the females ceasing to nurse, they start ovulating.\*

That's the male perspective. What about the females? They're also into maximizing copies of genes passed on. They fight the new male, protecting their infants. Females have also evolved the strategy of going into "pseudoestrus"—falsely appearing to be in heat. They mate with the male. And since males know squat about female langur biology, they fall for it—"Hey, I mated with her this morning and now she's got an infant; I am one major stud." They'll often cease their infanticidal attacks.

Despite initial skepticism, competitive infanticide has been documented in similar circumstances in 119 species, including lions, hippos, and chimps.<sup>9</sup>

A variant occurs in hamsters; because males are nomadic, any infant a male encounters is unlikely to be his, and thus he attempts to kill it (remember that rule about never putting a pet male hamster in a cage with babies?). Another version occurs among wild horses and gelada baboons; a new male harasses pregnant females into miscarrying. Or suppose you're a pregnant mouse and a new, infanticidal male has arrived. Once you give birth, your infants will be killed, wasting all the energy of pregnancy. Logical response? Cut your losses with the "Bruce effect," where pregnant females miscarry if they smell a new male.<sup>10</sup>

Thus competitive infanticide occurs in numerous species (including among female chimps, who sometimes kill infants of unrelated females).<sup>11</sup> None of this makes sense outside of gene-based individual selection.

Individual selection is shown with heartbreaking clarity by mountain gorillas, my favorite primate.<sup>12</sup> They're highly endangered, hanging on in pockets of high-altitude rain forest on the borders of Uganda, Rwanda, and the Democratic Republic of the Congo. There are only about a thousand gorillas left, because of habitat degradation, disease caught from nearby humans, poaching, and spasms of warfare rolling across those borders. And also because mountain gorillas practice competitive infanticide. Logical for an individual intent on maximizing the copies of his genes in the next generation, but simultaneously

pushing these wondrous animals toward extinction. This isn't behaving for the good of the species.

## KIN SELECTION

To understand the next foundational concept, reflect on what it means to be related to someone and to pass on copies of “your” genes.

Suppose you have an identical twin, with the same genome as you. As a startling, irrefutable fact, in terms of the genes being passed on to the next generation, it doesn’t matter if you reproduce or sacrifice yourself so that your twin reproduces.

What about a full sibling who isn’t an identical twin? Recall from chapter 8 that you’d share 50 percent of your genes with him.\* Thus reproducing once and dying so that he reproduces twice are evolutionarily identical. Half sibling, 25 percent of genes in common, calculate accordingly. . . .

The geneticist J. B. S. Haldane, who, when asked if he’d sacrifice his life for a brother, is credited to have quipped, “I’ll gladly lay down my life for two brothers or eight cousins.” You can leave copies of your genes in the next generation by reproducing, but also by helping relatives reproduce, especially closer relatives. Hamilton formalized this with an equation factoring in the costs and benefits of helping someone, weighted by their degree of relatedness to you. This is the essence of kin selection.\* This explains the crucial fact that in countless species, whom you cooperate with, compete with, or mate with depends on their degree of relatedness to you.

Mammals first encounter kin selection soon after birth, reflecting something monumentally obvious: females rarely nurse someone else’s infants. Next, among numerous primates the mother of a newborn and an adolescent female may commence a relationship fraught with pluses and minuses—the mother occasionally lets the adolescent care for her offspring. For the mother the plus is getting time to forage without baby on board; the minus is that the babysitter may be incompetent. For the adolescent the plus is getting mothering experience; the minus, the effort of child care. Lynn Fairbanks of UCLA has quantified the pluses and minuses of such “allomothering” (including that adolescents who practiced mothering have a better survival rate for their own kids). And who is a frequent “allomother”? The female’s kid sister.<sup>13</sup>

An extension of allomothering is the cooperative breeding of New World monkeys like marmosets. In their social groups only one female breeds, while the others—typically younger relatives—help with child care.<sup>14</sup>

The extent to which a male primate cares for infants reflects his certainty of paternity.<sup>15</sup> Among marmosets, who form stable pair-bonds, males do most of the child care. In contrast, among baboons, where a female mates with multiple males during her estrus cycle, it's only the likely fathers (i.e., males who mated on the female's most fertile day, when she had her most conspicuous estrus swelling) who invest in the well-being of the child, aiding him in a fight.\*

Among many primates, how often you groom someone depends on how closely related they are to you. Among baboons, females spend their whole life in their natal troop (whereas males migrate to a new troop at puberty); as a result, adult females have complex cooperative kinship relations and inherit their dominance rank from their mother. Among chimps it's the opposite; females leave home at puberty, and kin-based adult cooperation occurs only among males (for example, where groups of related males attack solitary males from neighboring groups). And among langurs, when a female defends her infant against a new male, she most often is helped by elderly female relatives.

Moreover, primates understand kinship. Dorothy Cheney and Robert Seyfarth of the University of Pennsylvania, studying wild vervet monkeys, have shown that if animal A is crummy to animal B, afterward, B is more likely to be crummy to A's *relatives*. And if A is lousy to B, B's *relatives* are more likely to be crummy to A. Furthermore, if A is lousy to B, B's relatives are more likely to be crummy to A's *relatives*.<sup>16</sup>

In beautiful “playback” experiments, Cheney and Seyfarth first recorded vocalizations from each vervet in a group. They'd place a speaker in some bushes, and when everyone was sitting around, they'd play a recording of some kid giving a distress call. And the females would all look at the kid's mother —“Hey, that's Madge's kid. What's she going to do?” (Note that this also shows that monkeys recognize voices.)

In a study of wild baboons, Cheney and Seyfarth would wait for two unrelated females to sit near the bush with the speaker and then play one of three vocalizations: (a) sounds of the two females' relatives fighting with each other; (b) a relative of one fighting with a third party; (c) two other random females fighting.<sup>17</sup> If a female's relative was involved in the fighting, she'd look toward the speaker longer than if there were no relatives involved. And if it was

relatives of the two females fighting each other, the higher-ranking one would remind the subordinate of her place by supplanting her from her spot.

Another playback study created some baboon virtual reality.<sup>18</sup> Baboon A dominates baboon B. Thanks to cutting and splicing of recordings of vocalizations, baboon A is heard making a dominance vocalization, B making a subordination one. When this happens, no baboons looked at the bushes—A > B, boring status quo. But if baboon A is heard making a *subordination* vocalization after B makes a *dominance* one—a rank reversal—everyone orients to the bushes (“Did you hear what I just heard?”). Then a third scenario—a dominance reversal between two members of the same family. And no one looks, because it’s uninteresting. (“Families, they’re crazy. You should see mine—we have these huge dominance reversals and are hugging an hour later.”) Baboons “classify others simultaneously according to both individual rank and kinship.”

Thus other primates contemplate kinship with remarkable sophistication, with kinship determining patterns of cooperation and competition.

Nonprimates are also into kin selection. Consider this—sperm in a female’s vaginal tract can aggregate, allowing them to swim faster. Among a deer mouse species where females mate with multiple males, sperm aggregate only with sperm from the same individual or a close relative.<sup>19</sup>

As behavioral examples, squirrels and prairie dogs give alarm vocalizations when spotting a predator. It’s risky, calling attention to the caller, and such altruism is more common when in the proximity of relatives. Social groups built around female relatives occur in numerous species (e.g., lion prides, where related females nurse one another’s cubs). Moreover, while prides typically contain a single breeding male, on those occasions when it’s two males, better than chance that they’re brothers. There is a striking similarity in humans. Most cultures have historically allowed polygyny, with monogamy as the rarer beast. Even rarer is polyandry—multiple men married to one woman. This occurs in northern India, Tibet, and Nepal, where the polyandry is “adelphic” (aka “fraternal”)—a woman marries all the brothers of one family, from the strapping young man to his infant brother.\*<sup>20</sup>

---

A challenging implication of kin selection arises.

*Those hot cousins.* If one accrues fitness benefits by helping relatives pass on copies of their genes, why not help them do that by mating with them? Yech; inbreeding produces decreased fertility and those genetic unpleasantnesses in

European royalty.<sup>21</sup> So the dangers of inbreeding counter the kin-selection advantages. Theoretical models suggest that the optimal balance is third-cousin matings. And indeed, numerous species prefer to mate with between a first and a third cousin.<sup>22</sup>

This occurs in insects, lizards, and fish, where, on top of that, cousin-mating pairs invest more in the rearing of their offspring than do unrelated parents. A preference for cousin matings occurs in quail, frigate birds, and zebra finches, while among pair-bonded barn swallows and ground tits, females sneak out on their partner to mate with cousins. Similar preferences occur in some rodents (including the Malagasy giant jumping rat, a species that sounds disturbing even without cousins shacking up with each other).<sup>23</sup>

And what about humans? Something similar. Women prefer the smell of moderately related over unrelated men. And in a study of 160 years of data concerning every couple in Iceland (which is a mecca for human geneticists, given its genetic and socioeconomic homogeneity), the highest reproductive success arose from third- and fourth-cousin marriages.<sup>24</sup>

## ***Recognizing Relatives?***

These findings concerning kin selection require animals to recognize degrees of relatedness. How do they do this?

Some species have innate recognition. For example, place a mouse in an arena; at one end is an unrelated female, at the other, a full sister from a different litter, never encountered before. The mouse spends more time with the sister, suggesting genetically based kin recognition.

How does this work? Rodents produce pheromonal odors with individual signatures, derived from genes called the major histocompatibility complex (MHC). This is a super variable gene cluster that produces unique proteins that form a signature for an individual. This was first studied by immunologists. What does the immune system do? It differentiates between you and invaders —“self” and “nonself”—and attacks the latter. All your cells carry your unique MHC-derived protein, and surveillance immune cells attack any cell lacking this protein password. And MHC-derived proteins also wind up in pheromones, producing a distinctive olfactory signature.

This system can indicate that this mouse is John Smith. How does it also tell that he’s your never-before-encountered brother? The closer the relative, the

more similar their cluster of MHC genes and the more similar their olfactory signature. Olfactory neurons in a mouse contain receptors that respond most strongly to the mouse's own MHC protein. Thus, if the receptor is maximally stimulated, it means the mouse is sniffing its armpit. If near maximally stimulated, it's a close relative. Moderately, a distant relative. Not at all (though the MHC protein is being detected by other olfactory receptors), it's a hippo's armpit.\*

Olfactory recognition of kin accounts for a fascinating phenomenon. Recall from chapter 5 how the adult brain makes new neurons. In rats, pregnancy triggers neurogenesis in the olfactory system. Why there? So that olfactory recognition is in top form when it's time to recognize your newborn; if the neurogenesis doesn't occur, maternal behavior is impaired.<sup>25</sup>

Then there is kin recognition based on imprinted sensory cues. How do I know which newborn to nurse? The one who smells like my vaginal fluid. Which kid do I hang out near? The one who smells like Mom's milk. Many ungulates use such rules. So do birds. Which bird do I know is Mom? The bird whose distinctive song I learned before hatching.

And there are species that figure out relatedness by reasoning; my guess is that male baboons make statistical inferences when identifying their likely offspring: "How much of this mom's peak estrus swelling was spent with me? All. Okay, this is my kid; act accordingly." Which brings us to the most cognitively strategic species, namely us. How do we do kin recognition? In ways that are far from accurate, with interesting consequences.

We start with a long theorized type of pseudo-kin recognition. What if you operate with the rule that you cooperate with (i.e., act related to) individuals who share conspicuous traits with you? This facilitates passing on copies of genes if you possess a gene (or genes) with three properties: (a) it generates that conspicuous signal; (b) recognizes it in others; and (c) makes you cooperate with others who have that signal. It's a kind of primitive, stripped-down kin selection.

Hamilton speculated about the existence of such a "green-beard effect"; if an organism has a gene that codes for both growing a green beard and cooperating with other green bearders, green bearders will flourish when mixed with non-green bearders.<sup>26</sup> Thus, "the crucial requirement for altruism is genetic relatedness at the altruism locus [i.e., merely a multifaceted green-beard gene] and not genealogical relationship over the whole genome."<sup>27</sup>

Green-beard genes exist. Among yeast, cells form cooperative aggregates that need not be identical or even closely related. Instead, it could be any yeast

that expresses a gene coding for a cell-surface adhesion protein that sticks to copies of the same molecule on other cells.<sup>[28](#)</sup>

Humans show green-beard effects. Crucially, we differ as to what counts as a green-beard trait. Define it narrowly, and we call it parochialism. Include enmity toward those without that green-beard trait and it's xenophobia. Define the green-beard trait as being a member of your species, and you've described a deep sense of humanity.



## RECIPROCAL ALTRUISM

So sometimes a chicken is an egg's way of making another egg, genes can be selfish, and sometimes we gladly lay down our lives for two brothers or eight cousins. Does everything have to be about competition, about individuals or groups of relatives leaving *more* copies of their genes than the others, being *more* fit, having *more* reproductive success? [\\*](#) Is the driving force of behavioral evolution always that someone be vanquished?

Not at all. One exception is elegant, if specialized. Remember rock/paper/scissors? Paper envelops rock; rock breaks scissors; scissors cut paper. Would rocks want to bash every scissors into extinction? No way. Because then all those papers would enwrap the rocks into extinction. Each participant has an incentive for restraint, producing an equilibrium.

Remarkably, such equilibriums occur in living systems, as shown in a study of the bacteria *Escherichia coli*.<sup>[29](#)</sup> The authors generated three colonies of *E. coli*, each with a strength and a weakness. To simplify: Strain 1 secretes a toxin. Strength: it can kill competitor cells. Weakness: making the toxin is energetically costly. Strain 2 is vulnerable to the toxin, in that it has a membrane transporter that absorbs nutrients, and the toxin slips in via that transporter. Strength: it's good at getting food. Weakness: vulnerability to the toxin. Strain 3 doesn't have the transporter and thus isn't vulnerable to the toxin, and it doesn't make the toxin. Strength: it doesn't bear the cost of making the toxin and is insensitive to it. Weakness: it doesn't absorb as much nutrients. Thus, destruction of strain 2 by strain 1 causes the demise of strain 1 thanks to strain 3. The study showed that the strains could exist in equilibrium, each limiting its growth.

Cool. But it doesn't quite fit our intuitions about cooperation. Rock/paper/scissors is to cooperation as peace due to nuclear weapons-based mutually assured destruction is to the Garden of Eden.

Which raises a third fundamental, alongside individual selection and kin selection: reciprocal altruism. "I'll scratch your back if you scratch mine. I'd rather not actually scratch yours if I can get away with it. And I'm watching you in case you try the same."

Despite what you might expect from kin selection, unrelated animals frequently cooperate. Fish swarm in a school, birds fly in formation. Meerkats take risks by giving alarm calls that aid everyone, vampire bats who maintain communal colonies feed one another's babies.<sup>\*30</sup> Depending on the species, unrelated primates groom one another, mob predators, and share meat.

Why should nonrelatives cooperate? Because many hands lighten the load. School with other fish, and you're less likely to be eaten (competition for the safest spot—the center—produces what Hamilton termed the “geometry of the selfish herd”). Birds flying in a V formation save energy by catching the updraft of the bird in front (raising the question of who gets stuck there).<sup>31</sup> If chimps groom one another, there are fewer parasites.

In a key 1971 paper biologist Robert Trivers laid out the evolutionary logic and parameters by which unrelated organisms engage in “reciprocal altruism”—incurring a fitness cost to enhance a nonrelative's fitness, with the expectation of reciprocation.<sup>32</sup>

It doesn't require consciousness to evolve reciprocal altruism; back to the metaphor of the airplane wing in the wind tunnel. But there are some requirements for its occurrence. Obviously, the species must be social. Furthermore, social interactions have to be frequent enough that the altruist and the indebted are likely to encounter each other again. And individuals must be able to recognize each other.

Amid reciprocal altruism occurring in numerous species, individuals often attempt to cheat (i.e., to not reciprocate) and monitor attempts by others to do the same to them. This raises the realpolitik world of cheating and counterstrategies, the two coevolving in escalating arms races. This is called a “Red Queen” scenario, for the Red Queen in *Through the Looking-Glass*, who must run faster and faster to stay in place.<sup>33</sup>

This raises two key interrelated questions:

- Amid the cold calculations of evolutionary fitness, when is it optimal to cooperate, when to cheat?
- In a world of noncooperators it's disadvantageous to be the first altruist. How do systems of cooperation ever start?<sup>\*</sup>

## ***Gigantic Question #1: What Strategy for Cooperating Is Optimal?***

While biologists were formulating these questions, other scientists were already starting to answer them. In the 1940s “game theory” was founded by the polymath John von Neumann, one of the fathers of computer science. Game theory is the study of strategic decision making. Framed slightly differently, it’s the mathematical study of when to cooperate and when to cheat. The topic was already being explored with respect to economics, diplomacy, and warfare. What was needed was for game theorists and biologists to start talking. This occurred around 1980 concerning the Prisoner’s Dilemma (PD), introduced in chapter 3. Time to see its parameters in detail.

Two members of a gang, A and B, are arrested. Prosecutors lack evidence to convict them of a major crime but can get them on a lesser charge, for which they’ll serve a year in prison. A and B can’t communicate with each other. Prosecutors offer each a deal—inform on the other and your sentence is reduced. There are four possible outcomes:

- Both A and B refuse to inform on each other: each serves one year.
- Both A and B inform on each other: each serves two years.
- A informs on B, who remains silent: A walks free and B serves three years.
- B informs on A, who remains silent: B walks and A serves three years.

Thus, each prisoner’s dilemma is whether to be loyal to your partner (“cooperate”) or betray him (“defect”). The thinking might go, “Best to cooperate. This is my partner; he’ll also cooperate, and we’ll each serve only a year. But what if I cooperate and he stabs me in the back? He walks, and I’m in for three years. Better defect. But what if we both defect—that’s two years. But maybe defect, in case he cooperates . . .” Round and round.\*

If you play PD once, there is a rational solution. If you, prisoner A, defect, your sentence averages out to one year (zero years if B cooperates, two years if B defects); if you cooperate, the average is two years (one year if B cooperates,

three years if B defects). Thus you should defect. In single-round versions of PD, it's always optimal to defect. Not very encouraging for the state of the world.

Suppose there are two rounds of PD. The optimal strategy for the second round is just like in a single-round version—always defect. Given that, the first-round defaults into being like a single-round game—and thus, defect during it also.

What about a three-round game? Defect in the third, meaning that things default into a two-round game. In which case, defect in the second, meaning defect in the first.

It's always optimal to defect in round Z, the final round. And thus it's always optimal to defect in round Z-1, and thus round Z-2. . . . In other words, when two individuals play for a *known* number of rounds, the optimal strategy precludes cooperation.

But what if the number of rounds is unknown (an “iterated” PD)? Things get interesting. Which is when the game theorists and biologists met.

The catalyst was political scientist Robert Axelrod of the University of Michigan. He explained to his colleagues how PD works and asked them what strategy they'd use in a game with an unknown number of rounds. The strategies offered varied enormously, with some being hair-raisingly complicated. Axelrod then programmed the various strategies and pitted them against each other in a simulated massive round-robin tournament. Which strategy won, was most optimal?

It was provided by a mathematician at the University of Toronto, Anatol Rapoport; as the mythic path-of-the-hero story goes, it was the simplest strategy. Cooperate in the first round. After that, you do whatever the other player did in the previous round. It was called Tit for Tat. More details:

You cooperate (C) in the first round, and if the other player always cooperates (C), you both happily cooperate into the sunset:

*Example 1:*

You: C C C C C C C C C C . . . .

Her: C C C C C C C C C C . . . .

Suppose the other player starts cooperating but then, tempted by Satan, defects (D) in round 10. You cooperated, and thus you take a hit:

*Example 2:*

You: C C C C C C C C C C

Her: C C C C C C C C C D

Thus, you Tit for Tat her, punishing her in the next round:

*Example 3:*

You: C C C C C C C C C C D

Her: C C C C C C C C C D ?

If by then she's resumed cooperating, you do as well; peace returns:

*Example 4:*

You: C C C C C C C C C C D C C C . . .

Her: C C C C C C C C C D C C C C . . .

If she continues defecting, you do as well:

*Example 5:*

You: C C C C C C C C C C D D D D D . . .

Her: C C C C C C C C C D D D D D D . . .

Suppose you play against someone who always defects. Things look like this:

*Example 6:*

You: C D D D D D D D D D . . .

Her: D D D D D D D D D D . . .

This is the Tit for Tat strategy. Note that it can never win. Best case is a draw, if playing against another person using Tit for Tat or someone using an "always cooperate" strategy. Otherwise it loses by a small margin. Every other strategy would always beat Tit for Tat by a small margin. However, other strategies playing against each other can produce catastrophic losses. And when everything

is summed, Tit for Tat wins. It lost nearly every battle but won the war. Or rather, the peace. In other words, Tit for Tat drives other strategies to extinction.

Tit for Tat has four things going for it: Its proclivity is to cooperate (i.e., that's its starting state). But it isn't a sucker and punishes defectors. It's forgiving—if the defector resumes cooperating, so will Tit for Tat. And the strategy is simple.

Axelrod's tournament launched a zillion papers about Tit for Tat in PD and related games (more later). Then something crucial occurred—Axelrod and Hamilton hooked up. Biologists studying the evolution of behavior longed to be as quantitative as those studying the evolution of kidneys in desert rats. And here was this world of social scientists studying this very topic, even if they didn't know it. PD provided a framework for thinking about the strategic evolution of cooperation and competition, as Axelrod and Hamilton explored in a 1981 paper (famous enough that it's a buzz phrase—e.g., “How'd your lecture go today?” “Terrible, way behind schedule; I didn't even get to Axelrod and Hamilton”).<sup>34</sup>

As the evolutionary biologists started hanging with the political scientists, they inserted real-world possibilities into game scenarios. One addressed a flaw in Tit for Tat.

Let's introduce signal errors—a message is misunderstood, someone forgets to tell someone something, or there's a hiccup of noise in the system. Like in the real world.

There has been a signal error in round 5, with two individuals using a Tit for Tat strategy. This is what everyone means:

*Example 7:*

You: C C C C C

Her: C C C C C

But thanks to a signal error, this is what you think happened:

*Example 8:*

You: C C C C C

Her: C C C C D

You think, “What a creep, defecting like that.” You defect in the next round. Thus, what you think has happened:

*Example 9:*

You: C C C C C D

Her: C C C C D C

What she thinks is happening, being unaware of the signal error:

*Example 10:*

You: C C C C C D

Her: C C C C C C

She thinks, “What a creep, defecting like that.” Thus she defects the next round. “Oh, so you want more? I’ll give you more,” you think, and defect. “Oh, so you want more? I’ll give you more,” she thinks:

*Example 11:*

You: C C C C C D C D C D C D C D C D . . .

Her: C C C C D C D C D C D C D C D C . . .

When signal errors are possible, a pair of Tit for Tat players are vulnerable to being locked forever in this seesawing of defection.\*

The discovery of this vulnerability prompted evolutionary biologists Martin Nowak of Harvard, Karl Sigmund of the University of Vienna, and Robert Boyd of UCLA to provide two solutions.<sup>35</sup> “Contrite Tit for Tat” retaliates only if the other side has defected twice in a row. “Forgiving Tit for Tat” automatically forgives one third of defections. Both avoid doomsday signal-error scenarios but are vulnerable to exploitation.\*

A solution to this vulnerability is to shift the frequency of forgiveness in accordance with the likelihood of signal error (“Sorry I’m late again; the train was delayed” being assessed as more plausible and forgivable than “Sorry I’m late again; a meteorite hit my driveway *again*”).

Another solution to Tit for Tat’s signal-error vulnerability is to use a shifting strategy. At the beginning, in an ocean of heterogeneous strategies, many heavily biased toward defection, start with Tit for Tat. Once they’ve become extinct, switch to Forgiving Tit for Tat, which outcompetes Tit for Tat when signal errors occur. What is this transition from hard-assed, punitive Tit for Tat to incorporating forgiveness? Establishing trust.

Other elaborations simulate living systems. The computer scientist John Holland of the University of Michigan introduced “genetic algorithms”—strategies that mutate over time.

Another real-world elaboration was to factor in the “cost” of certain strategies—for example, with Tit for Tat, the costs of monitoring for and then punishing cheating—costly alarm systems, police salaries, and jail construction. These are superfluous in a world of no signal errors and nothing but Tit for Taters, and Tit for Tat can be replaced by the cheaper Always Cooperate.

Thus, when there are signal errors, differing costs to different strategies, and the existence of mutations, a cycle emerges: a heterogeneous population of strategies, including exploitative, noncooperative ones, are replaced by Tit for Tat, then replaced by Forgiving Tit for Tat, then by Always Cooperate—until a mutation reintroduces an exploitative strategy that spreads like wildfire, a wolf among Always Cooperate sheep, starting the cycle all over again. . . .<sup>\*36</sup> More and more modifications made the models closer to the real world. Soon the computerized game strategies were having sex with each other, which must have been the most exciting thing ever for the mathematicians involved.

The evolutionary biologists were delighted to generate increasingly sophisticated models with the theoretical economists and theoretical diplomats and theoretical war strategists. The real question was whether animal behavior actually fits any of these models.

One bizarre animal system suggests Tit for Tat enforcement of cooperation involving the black hamlet fish, which form stable pair-bonds.<sup>37</sup> Nothing strange there. The fish can change sex (something that occurs in some fish species). As per usual, reproduction is more metabolically costly for the female than the male. So the fish in a pair take turns being the more expensive female. Say fish A and fish B have been doing their sex-change tango, and most recently A was the expensive female and B the cheap male. Suppose B cheats by staying male, forcing A to continue as female; A switches to male and stays that way until B regains his social conscience and becomes female.

Another widely cited study suggested a Tit for Tat strategy among stickleback fish.<sup>38</sup> The fish is in a tank, and on the other side of a glass partition is something scary—a bigger cichlid fish. The stickleback tentatively darts forward and back, investigating. Now put a mirror in its tank, perpendicular to the axis of the two fish. In other words, thanks to the mirror, there appears to be a *second* cichlid next to the first. Terrifying, except from out of nowhere there’s this mysterious second stickleback who checks out the second cichlid every time



our hero checks out the first—“I have no idea who this guy is, but we’re an amazing, coordinated team.”

Now convince the stickleback his partner is defecting. Angle the mirror so that the stickleback’s reflection is deflected backward. Now when the fish darts forward, his reflection does as well, but—that *jerk!*—it looks like he’s hanging back safely (lagging back even half a body length decreases the likelihood of a fish being predated). When the fish believes his partner is defecting, he stops darting forward.

Greater complexity in Tit for Tat-ing is suggested by some animals having multiple roles in their social groups.<sup>39</sup> Back to the playback technique with lions, where the roar of a strange male emanated from a speaker in the bushes (or from a life-sized model of a lion). Lions tentatively came forward to investigate, a risky proposition. Consistently, certain lions hung back. The toleration of these habitual scaredy-cats seemed to violate the demands of reciprocity, until it was recognized that such animals took the lead in other domains (e.g., in hunts). A similar punch line emerges concerning the Damaraland mole rat. The social groups of it and its relative, the naked mole rat, resemble those of social insects, with nonreproductive workers and a single breeding queen.\* Researchers noted some workers who never worked and were considerably fatter than the rest. It turns out that they have two specialized jobs—during the rains, they dig through flooded, collapsed tunnels of the burrows, and when necessary, they disperse with the risky task of starting a new colony.

I’m not convinced that a Tit for Tat reciprocity has been clearly demonstrated in other species. But evidence of its strict use would be hard for Martian zoologists to document in humans—after all, there are frequently pairs where one human does all the labor, the other doing nothing other than intermittently handing him some green pieces of paper. The point is that animals have systems of reciprocity with sensitivity to cheating.

## ***Gigantic Question #2: How Can Cooperation Ever Start?***

So a handful of Tit for Tat-ers can outcompete a mix of other strategies, including highly exploitative, uncooperative ones, losing the battles but winning the war. But what if there’s only one Tit for Tat-er in a population of ninety-nine Always Defect-ers? Tit for Tat doesn’t stand a chance. Always Defect-ers

playing each other produces the second-worst outcome for each. But a Tit for Tat—er playing an Always Defect—er does worse, getting the sucker payoff that first round before becoming a de facto Always Defect—er. This raises the second great challenge for reciprocal altruism: forget which strategy is best at fostering cooperation—how do you ever start *any* type? Amid a sea of Always Defect—ers, the first black hamlet fish, mole rat, or *Dictyostelium* amoeba who, after reading Gandhi, Mandela, Axelrod, and Hamilton, takes the first altruistic step is screwed, lagging behind everyone else forever. One can practically hear the Always Defect amoebas chortling derisively.

Let's make it slightly easier for Tit for Tat to gain a foothold. Consider two Tit for Tat—ers amid ninety-eight Always Defect—ers. Both will crash and burn . . . unless they find each other and form a stable cooperative core, where the Always Defect—ers either must switch to Tit for Tat or go extinct. A nidus of cooperation crystallizes outward through the population.

This is where green-beard effects help, conspicuous features of cooperators that help them recognize one another. Another mechanism is spatial, where the cooperative trait itself facilitates cooperators finding one another.

Another route has been suggested for jump-starting reciprocal altruism. Occasionally a geographic event occurs (say, a land bridge disappears), isolating a subset of a population for generations. What happens in such a “founder population”? Inbreeding, fostering cooperation via kin selection. Eventually the land bridge reappears, the inbred cooperative founder population rejoins the main group, and cooperation propagates outward.\*

We return to the issue of starting cooperation in the final chapter.

## STANDING ON THREE LEGS

**W**e've now seen the three foundations of thinking about the evolution of behavior—individual selection, kin selection, and reciprocal altruism. Moreover, we've seen how these three concepts can explain otherwise puzzling behaviors. Some concern individual selection, with competitive infanticide as the canonical example. Other behaviors are most explicable with kin selection—why there's male-male aggression between groups in only some primate species; why many species have hereditary ranking systems; why cousin matings are more frequent than one might expect. And some behaviors are all about reciprocal altruism. Why else would a vampire bat, aware of the vanquishing power of group selection, regurgitate blood for someone else's kid?

Let's consider a few more examples.

### ***Pair-Bonding Versus Tournament Species***

Suppose you've discovered two new species of primates. Despite watching both for years, here's all you know: In species A, male and females have similar body sizes, coloration, and musculature; in species B, males are far bigger and more muscular than females and have flashy, conspicuous facial coloration (jargon: species B is highly "sexually dimorphic"). We'll now see how these two facts allow you to accurately predict a ton of things about these species.



*Male-female pairs of tamarins (top) and mandrills (bottom)*

First off, which species has dramatic, aggressive conflict among males for high dominance rank? Species B, where males have been selected evolutionarily for fighting skills and display. Species A males, in contrast, are minimally aggressive—that's why males haven't been selected for muscle.

What about variability in male reproductive success? In one species 5 percent of the males do nearly all the mating; in the other, all males reproduce a few times. The former describes species B—that's what all the rank competition is about—the latter, species A.

Next, in one species, if a male mates with a female and she conceives, he'll do a ton of child care. In contrast, no such male "parental investment" is seen in the other species. No-brainer: the former describes species A; the few species B males who father most of the kids sure aren't doing child care.

One species has a tendency to twin, the other not. Easy—the twinning is in species A, with two sets of parental hands available.

How picky are males about whom they mate with? In species B, males mate with anyone, anywhere, anytime—it only costs the price of some sperm. In contrast, males of species A, with its rule of "You get her pregnant, you do child care," are more selective. Related to that, which species forms stable pair-bonds? Species A, of course.

After correcting for body size, which species' males have bigger testes and higher sperm count? It's species B, ever prepared for mating, should the opportunity arise.

What do females look for in a potential mate? Species B females get nothing from a male except genes, so they should be good ones. This helps explain the flamboyant secondary sexual characteristics of males—"If I can afford to waste all this energy on muscle plus these ridiculous neon antlers, I must be in great shape, with the sorts of genes you'd want in your kids." In contrast, species A females look for stable, affiliative behavior and good parenting skills in males. This is seen in bird species with this pattern, where males display parenting expertise during courtship—symbolically feeding the female with worms, proof that he'd be a competent worm winner. Related to that, among bird versions of species A and B, in which is a female more likely to abandon her offspring, passing on more copies of her genes by breeding with another male? Species A, where you see "cuckoldry"—because the male is going to stick there, caring for the kids.

Related to that, in species A, females compete aggressively to pair-bond with a particularly desirable (i.e., paternal) male. In contrast, species B females don't

need to compete, since all they get from males is sperm, and there's enough to go around from desirable males.

Remarkably, what we've described here is a broad and reliable dichotomy between two social systems, where A is a "pair-bonding" species, B a "tournament" species.<sup>[\\*](#)</sup>

	Pair-Bonded	Tournament
Male parental behavior	Extensive	Minimal
Male mating pickiness	High	Low
Variability in male reproductive success	Low	High
Testes size, sperm count	Small/low	Large/high
Levels of male-male aggression	Low	High
Degree of sexual dimorphism in body weight, physiology, coloration, and life span	Low	High
Females select for	Parenting skill	Good genes
Rates of cuckoldry	High	Low

Primates that pair-bond include South American monkeys like marmosets, tamarins, and owl monkeys, and among the apes, gibbons (with nonprimate examples including swans, jackals, beavers, and, of course, chapter 4's prairie voles). Classic tournament species include baboons, mandrills, rhesus monkeys, vervets, and chimps (with nonprimate examples including gazelles, lions, sheep, peacocks, and elephant seals). Not all species fit perfectly into either extreme (stay tuned). Nonetheless, the point is the internal logic with which the traits of each of these types of species cluster, based on these evolutionary principles.

## ***Parent-Offspring Conflict***

Another feature of behavior turns kin selection on its head. The emphasis until now has been on the fact that relatives share many genes and evolutionary goals. Nonetheless, except for identical twins, just as pertinent is relatives not sharing *all* their genes or goals. Which can cause conflict.

There's *parent-offspring conflict*. One classic example is whether a female should give her child great nutrition, guaranteeing his survival, but at the cost of nutrition for her other children (either current or future). This is weaning conflict.<sup>[40](#)</sup>

This causes endless primate tantrums.<sup>[41](#)</sup> Some female baboon looks frazzled and cranky. Three steps behind is her toddler, making the most pitiful

whimpering and whining sounds imaginable. Every few minutes the kid tries to nurse; Mom irritably pushes him away, even slaps him. More wailing. It's parent-offspring weaning conflict; as long as Mom nurses, she's unlikely to ovulate, curtailing her future reproductive potential. Baboon moms evolved to wean their kids at the age where they can feed themselves, and baboon kids evolved to try to delay that day. Interestingly, as females age, with decreasing likelihood of a future child, they become less forceful in weaning.\*

There's also mother-fetus conflict. You're a fetus with an evolutionary agenda. What do you want? Maximal nutrition from Mom, and who cares if that impacts her future reproductive potential? Meanwhile, Mom wants to balance current and future reproductive prospects. Remarkably, fetus and Mom have a metabolic struggle involving insulin, the pancreatic hormone secreted when blood glucose levels rise, which triggers glucose entry into target cells. The fetus releases a hormone that makes Mom's cells unresponsive to insulin (i.e., "insulin resistant"), as well as an enzyme that degrades Mom's insulin. Thus Mom absorbs less glucose from her bloodstream, leaving more for the fetus.\*

### ***Intersexual Genetic Conflict***

In some species the fetus has an ally during maternal/fetal conflict—the father. Consider a species where males are migratory, mating with females and then moving on, never to be seen again. What's a male's opinion about maternal/fetal conflict? Make sure the fetus, i.e., his child, grabs as much nutrition as possible, even if that lessens Mom's future reproductive potential—who cares, that won't be his kid down the line. He's more than just rooting for his fetus.

This helps explain a mysterious, quirky feature of genetics. Normally a gene works the same way, regardless of which parent it comes from. But certain rare genes are "imprinted," working differently, or only being activated, depending on the parent of origin. Their purpose was discovered in a creative synthesis by evolutionary biologist David Haig of Harvard. Paternal imprinted genes bias toward more fetal growth, while maternal imprinted genes counter this. For example, some paternal genes code for potent versions of growth factors, while the maternal genes code for growth factor receptors that are relatively unresponsive. A paternally derived gene expressed in the brain makes newborns more avid nursers; the maternally derived version counters this. It's an arms

race, with Dad genetically egging on his offspring toward more growth at the cost of the female's future reproductive plans, and Mom genetically countering this with a more balanced reproductive strategy.\*

Tournament species, where males have minimal investment in a female's future reproductive success, have numerous imprinted genes, while pair-bonders don't.<sup>42</sup> What about humans? Stay tuned.



## MULTILEVEL SELECTION

So we've got individual selection, kin selection, and reciprocal altruism. And then what happened in recent years? Group selection reappeared, sneaking in the back door.

“Neo-group selection” crashed a long-standing debate as to the “unit of selection.”

### ***Genotype Versus Phenotype, and the Most Meaningful Level of Selection***

To appreciate this, let's contrast *genotype* and *phenotype*. Genotype = someone's genetic makeup. Phenotype = the traits observable to the outside world produced by that genotype.\*

Suppose there's a gene that influences whether your eyebrows come in two separate halves or form a continuous unibrow. You've noted that unibrow prevalence is decreasing in a population. Which is the more important level for understanding why—the gene variant or the eyebrow phenotype? We know after chapter 8 that genotype and phenotype are not synonymous, because of gene/environment interactions. Maybe some prenatal environmental effect silences one version of the gene but not the other. Maybe a subset of the population belongs to a religion where you must cover your eyebrows when around the opposite sex, and thus eyebrow phenotype is untouched by sexual selection.

You're a grad student researching unibrow decline, and you must choose whether to study things at the genotypic or phenotypic level. Genotypic: sequencing eyebrow gene variants, trying to understand their regulation. Phenotypic: examining, say, eyebrow appearance and mate choice, or whether unibrows absorb more heat from sunlight, thereby damaging the frontal cortex, producing inappropriate social behavior and decreased reproductive success.

This was the debate—is evolution best understood by focusing on genotype or phenotype?

The most visible proponent of the gene-centered view has long been Dawkins, with his iconic “selfish gene” meme—it is the gene that is passed to the next generation, the thing whose variants spread or decline over time. Moreover, a gene is a clear and distinctive sequence of letters, reductive and irrefutable, while phenotypic traits are much fuzzier and less distinct.

This is the core of the concept of “a chicken is just an egg’s way of making another egg”—the organism is just a vehicle for the genome to be replicated in the next generation, and behavior is just this wispy epiphenomenon that facilitates the replication.

This gene-centered view can be divided in two. One is that the genome (i.e., the collection of all the genes, regulatory elements, and so on) is the best level to think about things. The more radical view, held by Dawkins, is that the most appropriate level is that of individual genes—i.e., selfish genes, rather than selfish genomes.

Amid some evidence for single-gene selection (an obscure phenomenon called intragenomic conflict, which we won’t go into), most people who vote for the importance of gene(s) over phenotype view single-gene selfishness as a bit of a sideshow and vote for the genome level of selection being most important.

Meanwhile, there’s the view that phenotype trumps genotype, something championed by Ernst Mayr, Stephen Jay Gould, and others. The core of their argument is that it’s phenotypes rather than genotypes that are selected for. As Gould wrote, “No matter how much power Dawkins wishes to assign to genes, there is one thing he cannot give them—direct visibility to natural selection.” In that view, genes and the frequencies of their variants are merely the record of what arose from phenotypic selection.<sup>43</sup>

Dawkins introduced a great metaphor: a cake recipe is a genotype, and how the cake tastes is the phenotype.\* Genotype chauvinists emphasize that the recipe is what is passed on, the sequence of words that make for a stable replicator. But people select for taste, not recipe, say the phenotypists, and taste reflects more than just the recipe—after all, there are recipe/environment



interactions where bakers differ in their skill levels, cakes bake differently at various altitudes, etc. The recipe-versus-taste question can be framed practically: Your cake company isn't selling enough cakes. Do you change the recipe or the baker?

Can't we all get along? There's the obvious bleeding-heart answer, namely that there's room for a range of views and mechanisms in our rainbow-colored tent of evolutionary diversity. Different circumstances bring different levels of selection to the forefront. Sometimes the most informative level is the single gene, sometimes the genome, sometimes a single phenotypic trait, sometimes the collection of all the organism's phenotypic traits.<sup>44</sup> We've just arrived at the reasonable idea of multilevel selection.

### ***The Resurrection of Group Selection***

Hooray, progress. Sometimes it makes the most sense to pay attention to the recipe, sometimes to the baking process; the recipe is what is replicated, the taste what is chosen.

But there's another level. Sometimes cake sales can be changed most consequentially by altering something other than recipe or taste—advertisements, packaging, or the perception of whether the cake is a staple or a luxury. Sometimes sales are changed by tying the product to a particular audience—think of products that advertise fair-trade practices, the Nation of Islam's Your Black Muslim Bakery, or the Christian fundamentalist ideology of Chick-fil-A restaurants. And in those cases recipe and taste can both be trumped by ideology in purchasing decisions.

This is where neo-group selection fits into multilevel selection—the idea that some heritable traits may be maladaptive for the individual but adaptive for a group. This has cooperation and prosociality written all over it, straight out of the analysis of Tit for Tat-ers finding one another in a sea of Always Defect-ers. Stated more formally, it's when A dominates B but a *group* of Bs dominates a group of As.

Here's a great example of neo-group selectionism: As a poultry farmer, you want your groups of chickens to lay as many eggs as possible. Take the most prolific egg layer in each group, forming them into a group of superstar chickens who, presumably, will be hugely productive. Instead, egg production is miniscule.<sup>45</sup>

Why was each superstar the egg queen in her original group? Because she would aggressively peck subordinates enough to stress them into reduced fertility. Put all these mean ones together, and a group of subordinated chickens will outproduce them.

This is a world away from “animals behave for the good of the species.” Instead, this is the circumstance of a genetically influenced trait that, while adaptive on an individual level, emerges as maladaptive when shared by a group and where there is competition between groups (e.g., for an ecological niche).

There’s been considerable resistance to neo-group selectionism. Part of it is visceral, often pronounced among the old guard—“Great, we’ve finally confiscated all the *Wild Kingdom* videos, and now we’re back to playing Whac-A-Mole with group selection sentimentality?” But the more fundamental resistance is from people who distinguish bad old group selection from neo-group selection, accept that the latter can occur, but think it’s very rare.

Maybe so, across the animal kingdom. But neo-group selection plays out with great frequency and consequence in humans. Groups compete for hunting grounds, pastures, water sources. Cultures magnify the intensity of between-group selection and lessen within-group selection with ethnocentrism, religious intolerance, race-based politics, and so on. The economist Samuel Bowles, of the Santa Fe Institute, emphasizes how intergroup conflict like war is the driving force for intragroup cooperation (“parochial altruism”); he refers to intergroup conflict as “altruism’s midwife.”<sup>46</sup>

Most in the field now both accept multilevel selection and see room for instances of neo-group selection, especially in humans. Much of this reemergence is the work of two scientists. The first is David Sloan Wilson of the State University of New York at Binghamton, who spent decades pushing for neo-group selection (although he sees it not really as “neo” but rather as old-style group selection finally getting some scientific rigor), generally being dismissed, and arguing his case with research of his own, studies ranging from fish sociality to the evolution of religion. He slowly convinced some people, most importantly the second scientist, Edward O. Wilson of Harvard (no relation). E. O. Wilson is arguably the most important naturalist of the last half of the twentieth century, an architect of the sociobiology synthesis along with a number of other fields, a biology god. E. O. Wilson had long dismissed David Sloan Wilson’s ideas. And then a few years back, the octogenarian E. O. Wilson did something extraordinary—he decided he was wrong. And then he published a key paper with the other Wilson—“Rethinking the Theoretical Foundation of

Sociobiology.” My respect for these two, both as people and as scientists, is enormous.<sup>[47](#)</sup>

Thus something resembling détente has occurred among the advocates for the importance of differing levels of selection. Our three-legged chair of individual selection, kin selection, and reciprocal altruism seems more stable with four legs.

## AND US

Where do humans fit into all this? Our behavior closely matches the predictions of these evolutionary models. Until you look more closely.<sup>48</sup>

Let's start by clearing up some misconceptions. First, we are not descended from chimps. Or from any extant animal. We and chimps share a common ancestor from roughly five million years ago (and genomics show that chimps have been as busy evolving since then as we have).<sup>49</sup>

And there are misconceptions as to which ape is our "closest relative." In my experience, someone who is fond of duck hunting and country music usually votes chimp, but if you eat organic food and know about oxytocin, it's bonobo. The reality is that we're equally related to both, sharing roughly 98 to 99 percent of our DNA with each. Svante Pääbo of the Max Planck Institutes in Germany has shown that 1.6 percent of the human genome is more related to bonobos than to chimps; 1.7 percent more to chimps than to bonobos.<sup>\*50</sup> Despite the combination of some of our most fervent wishes and excuses, we're neither bonobos nor chimps.

On to how the conceptual building blocks of behavioral evolution apply to humans.

### ***Promiscuous Tournament or Monogamous Pair-Bonded?***

I can't resist starting with an irresistible question—so, are we a pair-bonded or tournament species?<sup>51</sup>

Western civilization doesn't give a clear answer. We praise stable, devoted relationships yet are titillated, tempted, and succumb to alternatives at a high rate. Once divorces are legalized, a large percentage of marriages end in them, yet a smaller percentage of married people get divorced—i.e., the high divorce rate arises from serial divorcers.

Anthropology doesn't help either. Most cultures have allowed polygyny. But within such cultures most people are (socially) monogamous. But most of those

men would presumably be polygamous if they could buy more wives.

What about human sexual dimorphism? Men are roughly 10 percent taller and 20 percent heavier than women, need 20 percent more calories, and have life spans 6 percent shorter—more dimorphic than monogamous species, less than polygamous ones. Likewise with subtle secondary sexual characteristics like canine length, where men average slightly longer canines than women. Moreover, compared with, say, monogamous gibbons, human males have proportionately bigger testes and higher sperm counts . . . but pale in comparison with polygamous chimps. And back to imprinted genes, reflecting intersexual genetic competition, which are numerous in tournament species and nonexistent in pair-bonders. What about humans? Some such genes, but not many.

Measure after measure, it's the same. We aren't classically monogamous or polygamous. As everyone from poets to divorce attorneys can attest, we are by nature profoundly confused—mildly polygynous, floating somewhere in between.\*

## ***Individual Selection***

At first pass we seem like a great example of a species where the driving force on behavior is maximizing reproductive success, where a person can be an egg's way of making another egg, where selfish genes triumph. Just consider the traditional perk of powerful men: being polygamous. Pharaoh Ramses II, incongruously now associated with a brand of condoms, had 160 children and probably couldn't tell any of them from Moses. Within half a century of his death in 1953, Ibn Saud, the founder of the Saudi dynasty, had more than three thousand descendants. Genetic studies suggest that around sixteen million people today are descended from Genghis Khan. And in recent decades more than one hundred children each were fathered by King Sobhuza II of Swaziland, Ibn Saud's son King Saud, the dictator Jean-Bédél Bokassa of the Central African Republic, plus various fundamentalist Mormon leaders.<sup>52</sup>

The human male drive to maximize reproductive success is shown by a key fact—the most common cause of individual human violence is male-male competition for direct or indirect reproductive access to females. And then there is the dizzyingly common male violence against females for coercive sex or as a response to rejection.



So plenty of human behaviors would make sense to a baboon or elephant seal. But that's only half the story. Despite Ramses, Ibn Saud, and Bokassa, numerous people forgo reproducing, often because of theology or ideology. And an entire sect—the United Society of Believers in Christ's Second Appearing, aka the Shakers, will soon be extinct because of its adherents' celibacy. And finally, the supposed selfishness of human genes driving individual selection must accommodate individuals sacrificing themselves for strangers.

Earlier in the chapter I presented competitive infanticide as stark evidence of the importance of individual selection. Does anything like that occur in humans? The psychologists Martin Daly and (the late) Margo Wilson of McMaster University in Canada looked at patterns of child abuse and made a striking observation—a child is far more likely to be abused or killed by a stepparent than by a parent. This is readily framed as parallel to competitive infanticide.<sup>53</sup>

This finding, termed the “Cinderella effect,” while embraced by human sociobiologists, has also been robustly criticized. Some charge that socioeconomic status was not sufficiently controlled for (homes with a stepparent, rather than two biological parents, generally have less income and more economic stress, known causes of displacement aggression). Others think there's a detection bias—the same degree of abuse is more likely to be identified by authorities when it's committed by a stepparent. And the finding has been independently replicated in some but not all studies. I think the jury is still out on the subject.

## ***Kin Selection***

Where do humans fit in terms of kin selection? We've already seen examples that fit well—e.g., the fraternal polyandry in Tibet, the weirdness of women liking the smell of their male cousins, the universality of nepotism.

Moreover, humans are obsessed with kin relations in culture after culture, with elaborate systems of kinship terms (just go into a store and look at the Hallmark cards organized by kinship category—for a sister, a brother, an uncle, and so on). And in contrast to other primates who leave their natal group around adolescence, when humans in traditional society marry someone from another group and go live with them, they maintain contact with their family of origin.<sup>54</sup>

Moreover, from New Guinea highlanders to the Hatfields and McCoys, feuds and vendettas occur along clan lines of relatedness. We typically bequeath our



money and land among our descendants rather than among strangers. From ancient Egypt to North Korea and on to the Kennedys and Bushes, we have dynastic rule. How's this for a display of human kin selection: Subjects were given a scenario of a bus hurtling toward a human and a nondescript dog, and they could only save one. Whom would they pick? It depended on degree of relatedness, as one progressed from sibling (1 percent chose the dog over the sibling) to grandparent (2 percent) to distant cousin (16 percent) to foreigner (26 percent).<sup>55</sup>

As another measure of the importance of kinship in human interactions, people can't be compelled to testify in court against a first-degree relative in many countries and American states. And when humans have damage to the (emotional) vmPFC, they become so unemotionally utilitarian that they would choose to harm family members in order to save strangers.<sup>56</sup>

There's a fascinating historical example of how wrong it feels when someone chooses strangers over kin. This is the story of Pavlik Morozov, a boy in Stalin's Soviet Union.<sup>57</sup> Young Pavlik, according to the official story, was a model citizen, an ardent flag-waving patriot. In 1932 he chose the state over his kin, denouncing his father (for supposed black marketeering), who was promptly arrested and executed. Soon afterward the boy was killed, allegedly by relatives who felt more strongly about kin selection than he did.

The regime's propagandists embraced the story. Statues of the young martyr to the revolution were erected. Poems and songs were written; schools were named for him. An opera was composed, a hagiographic movie made.

As the story emerged, Stalin was told about the boy. And what was the response of the man most benefiting from such fealty to the state? Was it "If only all my citizens were that righteous; this lad gives me hope for our future"? No. According to historian Vejas Liulevicius of the University of Tennessee, when told about Pavlik, Stalin snorted derisively and said, "What a little pig, to have done such a thing to his own family." And then he turned the propagandists loose.

Thus even Stalin was of the same opinion as most mammals: something's wrong with that kid. Human social interactions are profoundly organized around kin selection; with the rare exception of a Pavlik Morozov, blood is thicker than water.

Naturally, until you look more closely.

For starters, yes, across cultures we are obsessed with kinship terms, but the terms often don't overlap with actual biological relatedness.

We certainly have clan vendettas, but we also have wars where combatants on opposing sides have higher degrees of relatedness than do fighters on the same side. Brothers fought on opposing sides in the Battle of Gettysburg.<sup>58</sup>

Relatives and their armies battle over royal succession; the cousins George V of England, Nicholas II of Russia, and Wilhelm II of Germany happily oversaw and sponsored World War I. And intrafamily individual violence occurs (although at extremely low rates when corrected for amount of time spent together). There's patricide, often an act of revenge for a long history of abuse, and fratricide. Rarely due to conflicts over issues of economic or reproductive importance—stolen birthrights of biblical proportion, someone sleeping with their sibling's spouse—fratricide is most often about long-standing irritants and disagreements that just happen to boil over into lethality (in early May 2016, for example, a Florida man was charged with second-degree murder in the killing of his brother—during a dispute over a cheeseburger). And then there is the hideous commonness of honor killings in parts of the world, as we've seen.<sup>59</sup>

The most puzzling cases of intrafamily violence, in terms of kin selection, are of parents killing children, a phenomenon most commonly arising from combined homicide/suicide, profound mental illness, or abuse that unintentionally proves fatal.<sup>\*60</sup> And then there are cases where a mother kills an unwanted child who is viewed as a hindrance—parent/offspring conflict flecked with the spittle of madness.<sup>61</sup>

While we bequeath money to our descendants, we also give charitably to strangers on the other side of the planet (thank you, Bill and Melinda Gates) and adopt orphans from other continents. (Sure, as we'll see in a later chapter, being charitable is tinged with self-interest, and most people who adopt kids do so because they cannot have biological offspring—but the occurrence of either act violates strict kin selection.) And in the primogeniture system of land inheritance, birth order trumps degree of relatedness.

Thus we have textbook examples of kin selection, but also dramatic exceptions.

Why do humans have such marked deviations from kin selection? I think this often reflects how humans go about recognizing relatives. We don't do it with certainty, by innate recognition of MHC-derived pheromones, the way rodents do (despite our being able to distinguish degrees of relatedness to some extent by smell). Nor do we do it by imprinting on sensory cues, deciding, "This person is my mother because I remember that her voice was the loudest when I was a fetus."

Instead we do kin recognition cognitively, by thinking about it. But crucially, not always rationally—as a general rule, we treat people like relatives when they *feel* like relatives.

One fascinating example is the Westermarck effect, demonstrated by marriage patterns among people raised in the Israeli kibbutz system.<sup>62</sup> Communal child rearing is central to the ethos of the traditional socialist agricultural kibbutz approach. Children know who their parents are and interact with them a few hours a day. But otherwise they live, learn, play, eat, and sleep with the cohort of kids their age in communal quarters staffed by nurses and teachers.

In the 1970s anthropologist Joseph Shepher examined records of all the marriages that had ever occurred between people from the same kibbutz. And out of the nearly three thousand occurrences, there was no instance of two individuals marrying who had been in the same age group during their first six years of life. Oh, people from the same peer group typically had loving, close, lifelong relationships. But no sexual attraction. “I love him/her to pieces, but am I attracted? Yech—he/she feels like my sibling.” Who feels like a relative (and thus not like a potential mate)? Someone with whom you took a lot of baths when you both were kids.

How’s this for irrationality? Back to people deciding whether to save the person or the dog. The decision depended not only on who the person was (sibling, cousin, stranger) but also on who the dog was—a strange dog or your own. Remarkably, 46 percent of women would save their dog over a foreign tourist. What would any rational baboon, pika, or lion conclude? That those women believe they are more related to a neotenized wolf than to another human. Why else act that way? “I’ll gladly lay down my life for eight cousins or my awesome labradoodle, Sadie.”

---

Human irrationality in distinguishing kin from nonkin takes us to the heart of our best and worst behaviors. This is because of something crucial—we can be *manipulated* into feeling more or less related to someone than we actually are. When it is the former, wonderful things happen—we adopt, donate, advocate for, empathize with. We look at someone very different from us and see similarities. It is called pseudokinship. And the converse? One of the tools of the propagandist and ideologue drumming up hatred of the out-group—blacks, Jews, Muslims, Tutsis, Armenians, Roma—is to characterize them as animals, vermin,

cockroaches, pathogens. So different that they hardly count as human. It's called pseudospeciation, and as will be seen in chapter 15, it underpins many of our worst moments.

### ***Reciprocal Altruism and Neo-Group Selectionism***

There's not much to say here other than that this is the most interesting stuff in the chapter. When Axelrod got his round-robin tournament all fired up, he didn't canvass, say, fish for their Prisoner's Dilemma strategies. He asked humans.

We're the species with unprecedented cooperation among unrelated individuals, even total strangers; *Dictyostelium* colonies are green with envy at the human ability to do a wave in a football stadium. We work collectively as hunter-gatherers or as IT execs. Likewise when we go to war or help disaster victims a world away. We work as teams to hijack planes and fly them into buildings, or to award a Nobel Peace Prize.

Rules, laws, treaties, penalties, social conscience, an inner voice, morals, ethics, divine retribution, kindergarten songs about sharing—all driven by the third leg of the evolution of behavior, namely that it is evolutionarily advantageous for nonrelatives to cooperate. Sometimes.

One manifestation of this strong human tendency has been appreciated recently by anthropologists. The standard view of hunter-gatherers was that their cooperative, egalitarian nature reflected high degrees of relatedness within groups—i.e., kin selection. The man-the-hunter version of hunter-gatherers viewed this as arising from patrilocality (i.e., where a woman, when marrying, moves to live with the group of her new husband), while the groovy-hunter-gatherers version tied it to matrilocality (i.e., the opposite). However, a study of more than five thousand people from thirty-two hunter-gatherer societies from around the world\* showed that only around 40 percent of people within bands are blood relatives.<sup>63</sup> In other words, hunter-gatherer cooperativeness, the social building block of 99 percent of hominin history, rests at least as much on reciprocal altruism among nonrelatives as on kin selection (with chapter 9's caveat that this assumes that contemporary hunter-gatherers are good stand-ins for ancestral ones).

So humans excel at cooperation among nonrelatives. We've already considered circumstances that favor reciprocal altruism; this will be returned to

in the final chapter. Moreover, it's not just groups of nice chickens outcompeting groups of mean ones that has revived group selectionism. It is at the core of cooperation and competition among human groups and cultures.

Thus humans deviate from the strict predictions concerning the evolution of behavior. And this is pertinent when considering three major criticisms of sociobiology.

## THE USUAL: WHERE ARE THE GENES?

I pointed out earlier a requirement for neo-group selection, namely that genes be involved in a trait that differs more between than within groups. This applies to everything in this chapter. The first requirement for a trait to evolve is that it be heritable. But this is often forgotten along the way, as evolutionary models tacitly assume genetic influences. Chapter 8 showed how tenuous is the idea that there is “the gene,” or even genes, “for” aggression, intelligence, empathy, and so on. Given that, even more tenuous would be the idea of a gene(s) for maximizing your reproductive success by, say, “mating indiscriminately with every available female,” or by “abandoning your kids and finding a new mate, because the father will raise them.”

So critics will often demand, “Show me the gene that you assume is there.” And sociobiologists will respond, “Show me a more parsimonious explanation than this assumption.”

## THE NEXT CHALLENGE: IS EVOLUTIONARY CHANGE CONTINUOUS AND GRADUAL?

The term “evolution” carries context-dependent baggage. If you’re in the Bible Belt, evolution is leftist besmirching of God, morality, and human exceptionalism. But to extreme leftists, “evolution” is a reactionary term, the slow change that impedes real change—“All reform undermines revolution.” This next challenge addresses whether evolution is actually more about rapid revolution than about slow reform.

A basic sociobiological premise is that evolutionary change is gradual, incremental. As a selective pressure gradually changes, a useful gene variant grows more common in a population’s gene pool. As enough changes accrue, the population may even constitute a new species (“phyletic gradualism”). Over millions of years, dinosaurs gradually turn into chickens, organisms emerge that qualify as mammals as glandular secretions slowly evolve into milk, thumbs increasingly oppose in proto-primates. Evolution is gradual, continuous.

In 1972 Stephen Jay Gould and paleontologist Niles Eldredge of the American Museum of Natural History proposed an idea that simmered and then caught fire in the 1980s. They argued that evolution isn’t gradual; instead, most of the time nothing happens, and evolution occurs in intermittent rapid, dramatic lurches.<sup>64</sup>

### ***Punctuated Equilibrium***

Their idea, which they called punctuated equilibrium, was anchored in paleontology. Fossil records, we all know, show gradualism—human ancestors show progressively larger skulls, more upright posture, and so on. And if two fossils in chronological progression differ a lot, a jump in the gradualism, there must be an intermediate form that is the “missing link” from a time between those two fossils. With enough fossils in a lineage, things will look gradualist.

Eldredge and Gould focused on there being plenty of fossil records that were complete chronologically (for example, trilobites and snails, Eldredge’s and

Gould's specialties, respectively) and didn't show gradualism. Instead there were long periods of stasis, of unchanged fossils, and then, in a paleontological blink of an eye, there'd be a rapid transition to a very different form. Maybe evolution is mostly like this, they argued. What triggers punctuated events of sudden change? A sudden, massive selective factor that kills most of a species, the only survivors being ones with some obscure genetic trait that turned out to be vital—an "evolutionary bottleneck."

Why does punctuated equilibrium challenge sociobiological thinking? Sociobiological gradualism implies that every smidgen of difference in fitness counts, that every slight advantage of one individual over another at leaving copies of genes in future generations translates into evolutionary change. At every juncture, optimizing competition, cooperation, aggression, parental investment, all of it, is evolutionarily consequential. And if instead there is mostly evolutionary stasis, much of this chapter becomes mostly irrelevant.\*

The sociobiologists were not amused. They called the punctuated equilibrium people "jerks" (while the punctuated equilibrium people called them "creeps"—get it? PE = evolution in a series of jerks; sociobiology = evolution as a gradual, creeping process).\* Gradualist sociobiologists responded with strong rebuttals, taking a number of forms:

*They're just snail shells.* First, there are some very complete fossil lineages that are gradualist. And don't forget, said the gradualists, these punctuated equilibrium guys are talking about trilobite and snail fossils. The fossil record we're most interested in—primates, hominins—is too spotty to tell if it is gradualist or punctuated.

*How fast do their eyes blink?* Next, said the gradualists, remember, these punctuated equilibrium fans are paleontologists. They see long periods of stasis and then extremely rapid blink-of-the-eye changes in the fossil record. But with fossils the blink of an eye, a stretch of time unresolvably short in the fossil record, could be 50,000 to 100,000 years. That's plenty of time for evolution bloody in tooth and claw to happen. This is only a partial refutation, since if a paleontological blink of the eye is so long, paleontological stasis is humongously long.

*They're missing the important stuff.* A key rebuttal is to remind everyone that paleontologists study things that are fossilized. Bones, shells, bugs in amber. Not organs—brains, pituitaries, ovaries. Not cells—neurons, endocrine cells, eggs, sperm. Not molecules—neurotransmitters, hormones, enzymes. In other words, none of the interesting stuff. Those punctuated equilibrium nudniks spend their



careers measuring zillions of snail shells and, based on that, say we're wrong about the evolution of behavior?

This opens the way for some compromise. Maybe the hominin pelvis did indeed evolve in a punctuated manner, with long periods of stasis and bursts of rapid change. And maybe the pituitary's evolution was punctuated as well, but with punctuations at different times. And maybe steroid hormone receptors and the organization of frontocortical neurons and the inventions of oxytocin and vasopressin all evolved that way also, but each undergoing punctuated change at a different time. Overlap and average these punctuated patterns, and it will be gradualist. This only gets you so far, though, since it assumes the occurrence of numerous evolutionary bottlenecks.

*Where's the molecular biology?* One of the strongest gradualist retorts was a molecular one. Micromutation, consisting of point, insertion, and deletion mutations that subtly change the function of preexisting proteins, is all about gradualism. But what mechanisms of molecular evolution explain rapid, dramatic change and long periods of stasis?

As we saw in chapter 8, recent decades have provided many possible molecular mechanisms for rapid change. This is the world of macromutations: (a) traditional point, insertion, and deletion mutations in genes whose proteins have amplifying network effects (transcription factors, splicing enzymes, transposes) in an exon expressed in multiple proteins in genes for enzymes involved in epigenetics; (b) traditional mutations in promoters, transforming the when/where/how-much of gene expression (remember that promoter change that makes polygamous voles monogamous); (c) untraditional mutations such as the duplication or deletion of entire genes. All means for big, rapid changes.

But what about a molecular mechanism for the stasis? Plunk a random mutation into a transcription-factor gene, thereby creating a new cluster of genes never before expressed simultaneously. What are the odds that it won't be a disaster? Randomly mutate a gene for an enzyme that mediates epigenetic changes, thereby producing randomly different patterns of gene silencing. Right, that's bound to work out swell. Parachute a transposable genetic element into the middle of some gene, change a splicing enzyme so that it mixes and matches different exons in multiple proteins. Both asking for major trouble. Implicit in this is stasis, a conservatism about evolutionary change—it takes very unique macro changes during times of very unique challenge to luck out.

*Show us some actual rapid change.* A final rebuttal from gradualists was to demand real-time evidence of rapid evolutionary change in species. And plenty

exist. One example was wonderful research by the Russian geneticist Dmitry Belyaev, who in the 1950s domesticated Siberian silver foxes.<sup>65</sup> He bred captive ones for their willingness to be in proximity to humans, and within thirty-five generations he'd generated tame foxes who'd cuddle in your arms. Pretty punctuated, I'd say. The problem here is that this is artificial rather than natural selection.



Interestingly, the opposite has occurred in Moscow, which has a population of thirty thousand feral dogs dating back to the nineteenth century (and where some contemporary dogs have famously mastered riding the Moscow subway system).<sup>66</sup> Most Moscow dogs are now descendants of generations of feral dogs, and over that time they have evolved to have a unique pack structure, avoid humans, and no longer wag their tails. In other words, they're evolving into something wolflike. Most likely, the first generations of these feral populations were subject to fierce selection for these traits, and it's their descendants who comprise the current population.<sup>\*67</sup>



*Feral Moscow dogs*

Rapid change in the human gene pool has occurred as well with the spread of lactase persistence—a change in the gene for the enzyme lactase, which digests lactose, such that it persists into adulthood, allowing adults to consume dairy.<sup>68</sup> The new variant is common in populations that subsist on dairy—pastoralists like Mongolian nomads or East African Maasai—and is virtually nonexistent in populations that don't use dairy after weaning—Chinese and Southeast Asians.

Lactase persistence evolved and spread in a fraction of a geologic blink of an eye—in the last ten thousand years or so, coevolving with domestication of dairy animals.

Other genes have spread in humans even faster. For example, a variant of a gene called ASPM, which is involved in cell division during brain development, has emerged and spread to about 20 percent of humans in the last 5,800 years.<sup>69</sup> And genes that confer resistance to malaria (at the cost of other diseases, such as sickle-cell disease or the thalassemias) are even younger.

Still, thousands of years counts as fast only for snail shell obsessives. However, evolution has been observed in real time. A classic example is the work of the Princeton evolutionary biologists Peter and Rosemary Grant, who, over the course of decades of work in the Galapagos, demonstrated substantial evolutionary change in Darwin's finches. Evolutionary change in humans has occurred in genes related to metabolism, when populations transition from traditional to Westernized diets (e.g., Pacific Islanders from Nauru, Native Americans of the Pima tribe in Arizona). The first generations with Westernized diets develop catastrophically high rates of obesity, hypertension, adult-onset diabetes, and death at early ages, thanks to “thrifty” genotypes that are great at storing nutrients, honed by millennia of sparser diets. But within a few generations diabetes rates begin to subside, as there is an increased prevalence in the population of “sloppier” metabolic genotypes.<sup>70</sup>

Thus, there are examples of rapid changes in gene frequencies in real time. Are there examples of gradualism? That's hard to show because gradual change is, er, gradual. A great example, however, comes from decades of work by Richard Lenski of Michigan State University. He has cultured *E. coli* bacteria colonies under constant conditions for 58,000 generations, roughly equivalent to a million years of human evolution. Over that time, different colonies have *gradually* evolved in distinctive ways, becoming more adapted.<sup>71</sup>

Thus, both gradualism and punctuated change occur in evolution, probably depending upon the genes involved—for example, there has been faster evolution of genes expressed in some brain regions than others. And no matter how rapid the changes, there's always some degree of gradualism—no female has ever given birth to a member of a new species.<sup>72</sup>

## A FINAL CHALLENGE LACED WITH POLITICS: IS EVERYTHING ADAPTIVE?

**A**s we've seen, variants of genes that make organisms more adapted to their environment increase in frequency over time. But what about the reverse—if a trait is prevalent in a population, must it mean that it evolved in the past *because* it was adaptive?<sup>73</sup>

“Adaptationism” assumes this is typically the case; an adaptationist approach is to determine whether a trait is indeed adaptive and, if so, what the selective forces were that brought it about. Much of sociobiological thinking is adaptationist in flavor.

This was subject to scathing criticism by the likes of Stephen Jay Gould and Harvard geneticist Richard Lewontin, who mocked the approach as “just so” stories, after Kipling’s absurdist fantasies about how certain traits came to be: how the elephant got its trunk (because of a tug-of-war with a crocodile), how the zebra got its stripes, how the giraffe got a long neck. So why not, supposedly ask the sociobiologists in this critique, how the baboon male got big cojones while the gorilla male got little ones? Observe a behavior, generate a just-so story that assumes adaptation, and the person with the best just-so story wins. How the evolutionary biologist got his tenure. In their view, sociobiological standards lack rigor. As one critic, Andrew Brown, stated, “The problem was that sociobiology explained too much and predicted too little.”<sup>74</sup>

According to Gould, traits often evolve for one reason and are later co-opted for another use (fancy term: “exaptation”); for example, feathers predate the evolution of bird flight and originally evolved for insulation.<sup>75</sup> Only later did their aerodynamic uses become relevant. Similarly, the duplication of a gene for a steroid hormone receptor (as mentioned many chapters ago) allowed one copy to randomly drift in its DNA sequence, producing an “orphan” receptor with no use—until a novel steroid hormone was synthesized that happened to bind to it. This haphazard, jury-rigged quality evokes the aphorism “Evolution is a tinkerer, not an inventor.” It works with whatever’s available as selective pressures change, producing a result that may not be the most adaptive but is good enough, given the starting materials. Squid are not great swimmers compared with



sailfish (maximum speed: sixty-eight miles per hour). But they're damn good for something whose great-great-grandparents were mollusks.

Meanwhile, ran the criticism, some traits exist not because they're adaptive, or were adapted for something else but got co-opted, but because they're baggage carried along with other traits that were selected for. It was here that Gould and Lewontin famously introduced "spandrels" in their 1979 paper "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." A spandrel is an architectural term for the space between two arches, and Gould and Lewontin considered the artwork on the spandrels of the Basilica San Marco in Venice.\*



Gould and Lewontin's stereotypical adaptationist would look at these spandrels and conclude that they were built to provide spaces for the artwork. In other words, that these spandrels evolved for their adaptive value in providing space for art. In reality they didn't evolve for a purpose—if you're going to have a series of arches (which most definitely exist for the adaptive purpose of holding up a dome), a space between each pair is an inevitable by-product. No adaptation. And as long as these spaces were carried along as evolutionary baggage as a result of selection for the adaptive arches, might as well paint on them. In that view, male nipples are spandrels—they serve an adaptive role in females and came along for the ride as baggage in males because there's been no particular

selection *against* males having them.\* Gould and Lewontin argued that numerous traits that prompted just-so stories from adaptationists are merely spandrels.

Sociobiologists responded to spandrelism by noting that the rigor in pronouncing something a spandrel was not intrinsically greater than that in pronouncing it adaptive.<sup>76</sup> In other words, the former provide just-*not*-so stories.

Psychologist David Barash and psychiatrist Judith Lipton compared spandrelites to the character Topsy in *Uncle Tom's Cabin*, who states that she “just grewed”—when faced with evidence of adaptation in traits, they’d conclude that those traits are mere baggage, without adaptive purpose, providing explanations that explained nothing—“just grewed stories.”

Furthermore, sociobiologists argued, adaptationist approaches were more rigorous than Gouldian caricature; rather than explaining everything and predicting nothing, sociobiological approaches predict plenty. Is, say, competitive infanticide a just-so story? Not when you can predict with some accuracy whether it will occur in a species based on its social structure. Nor is the pair-bond/tournament comparison, when you can predict a vast amount of information about the behavior, physiology, and genetics of species ranging across the animal kingdom simply by knowing their degree of sexual dimorphism. Furthermore, evolution leaves an echo of selection for adaptive traits when there is evidence of “special design”—complex, beneficial functions where a number of traits converge on the same function.

---

All this would be your basic, fun academic squabble, except that underlying the criticisms of adaptationism, gradualism, and sociobiology is a political issue. This is embedded in the title of the spandrel paper: the “Panglossian paradigm.” This refers to Voltaire’s Dr. Pangloss and his absurd belief, despite life’s miseries, that this is the “best of all possible worlds.” In this criticism, adaptationism stinks of the naturalistic fallacy, the view that if nature has produced something, it must be a good thing. That furthermore, “good” in the sense of, say, solving the selective problem of water retention in deserts, is in some indefinable way also morally “good.” That if ant species make slaves, if male orangutans frequently rape females, and if for hundreds of thousands of years hominin males drink milk directly out of the container, it is because it is somehow “meant” to be that way.

When aired as a criticism in this context, the naturalistic fallacy had an edge to it. In its early years human sociobiology was wildly controversial, with conferences picketed and talks disrupted, with zoologists guarded by police at lectures, all sorts of outlandish things. On one storied occasion, E. O. Wilson was physically attacked while giving a talk.\* Anthropology departments split in two, collegial relationships were destroyed. This was particularly so at Harvard,

where many of the principals could be found—Wilson, Gould, Lewontin, Trivers, Hrdy, the primatologist Irven DeVore, the geneticist Jonathan Beckwith.

Things were so febrile because sociobiology was accused of using biology to justify the status quo—conservative social Darwinism that implied that if societies are filled with violence, unequal distribution of resources, capitalistic stratification, male dominance, xenophobia, and so on, these things are in our nature and probably evolved for good reasons. The critics used the “is versus ought” contrast, saying, “Sociobiologists imply that when an unfair feature of life *is* the case, it is because it *ought* to be.” And the sociobiologists responded by flipping is/ought around: “We agree that life *ought* to be fair, but nonetheless, this *is* reality. Saying that we advocate something just because we report it is like saying oncologists advocate cancer.”

The conflict had a personal tinge. This was because by chance (or not, depending on your viewpoint), that first generation of American sociobiologists were all white Southerners—Wilson, Trivers,\* DeVore, Hrdy; in contrast, the first generation of its loudest critics were all Northeastern, urban, Jewish leftists—Harvard’s Gould, Lewontin, Beckwith, Ruth Hubbard, Princeton’s Leon Kamin, and MIT’s Noam Chomsky. You can see how the “there’s a hidden agenda here” charge arose from both sides.\*

It’s easy to see how punctuated equilibrium generated similar ideological battles, given its premise that evolution is mostly about long periods of stasis pierced by revolutionary upheaval. In their original publication, Gould and Eldredge asserted that the law of nature “holds that a new quality emerges in a leap as the slow accumulation of quantitative changes, long resisted by a stable system, finally forces it rapidly from one state into another.” This was a bold assertion that the heuristic of dialectical materialism not only extends beyond the economic world into the naturalistic one, but is ontologically rooted in the essential sameness of both worlds’ dynamic of resolution of irresolvable contradictions.\* It is Marx and Engels as trilobite and snail.\*

---

Eventually the paroxysms about adaptationism versus spandrels, gradualism versus punctuated change, and the very notion of a science of human sociobiology subsided. The political posturing lost steam, the demographic contrasts between the two camps softened, the general quality of research improved considerably, and everybody got some gray hair and a bit more calm.



This has paved the way for a sensible, middle-of-the-road middle age for the field. There's clear empirical evidence for both gradualism and punctuated change, and for molecular mechanisms underlying both. There's less adaptation than extreme adaptationists claim, but fewer spandrels than touted by spandrelites. While sociobiology may explain too much and predict too little, it does predict many broad features of behavior and social systems across species. Moreover, even though the notion of selection happening at the level of groups has been resurrected from the graves of self-sacrificial elderly wildebeest, it is probably a rare occurrence; nonetheless, it is most likely to occur in the species that is the focus of this book. Finally, all of this is anchored in evolution being a fact, albeit a wildly complex one.

---

Remarkably, we've finished this first part of the book. A behavior has occurred; what happened in everything from a second to a million years earlier that helps explain why it happened? Some themes have come up repeatedly:

- The context and meaning of a behavior are usually more interesting and complex than the mechanics of the behavior.
  - To understand things, you must incorporate neurons *and* hormones *and* early development *and* genes, etc., etc.
  - These aren't separate categories—there are few clear-cut causal agents, so don't count on there being *the* brain region, *the* neurotransmitter, *the* gene, *the* cultural influence, or *the* single anything that explains a behavior.
  - Instead of causes, biology is repeatedly about propensities, potentials, vulnerabilities, predispositions, proclivities, interactions, modulations, contingencies, if/then clauses, context dependencies, exacerbation or diminution of preexisting tendencies. Circles and loops and spirals and Möbius strips.
  - No one said this was easy. But the subject matters.
- 

And thus we transition to the second part, synthesizing this material in order to look at realms of behavior where this matters the most.