Racing the Red Queen:
Selfish Genes and Their Strategies

Now here, you see, it takes all the running you can get to do, to keep in
the same place. If you want to get somewhere else, you must run at least
twice as fast as that!
—The Red Queen in Lewis Carroll’s Through the Looking-Glass

ALICE HAD some trouble following the Red Queen’s logic, that one has to run as fast as one can just to stay in place because everything else in the landscape is running as well. Biologists, however, find the image an apt one. Consider Matt Ridley’s engaging book on the origins of sexual selection, which he chose to call The Red Queen in recognition of the problem that the sexes continually change each other’s costs and benefits. In a way, much of biology is a record of such selective arms races. Ecology is rife with examples: if faster rabbits escape coyotes, tomorrow’s rabbits are faster than today’s—but once this is true, fast rabbits put pressure on coyotes, so that faster or sneakier coyotes become the only successful ones. For us humans, our families, friends, and rivals are forces to be reckoned with. Such “social selection” (chapter 10) is surely a good example of the Red Queen’s problem: the goal you seek is situated in a moving landscape, and it may always be moving away from you.

At the core of behavioral ecology rests the notion Richard Dawkins aptly called the “selfish gene,” the idea that genes that get themselves copied into more and more individuals will be the genes that prevail and persist through time. This measure of success is a modern version of the simple logic first employed explicitly by Darwin. Genes compete for locations on the chromosome, and groups of genes make what biologist Leigh Van Valen called a “parliament”
(they interact to produce complex effects); individuals housing effective parliaments survive and reproduce relatively better than those who don’t.

At some level, this competition among genes is like the old adage, “I don’t have to outrun the bear; I only have to outrun you.” That is, no guarantees exist that the chance events of mutation, recombination, and drift, combined with the filtering of natural selection, have generated the best possible combinations; it is only true that, at any moment, relatively more effective combinations do better than others. Individuals thus never represent the “best conceivable” combinations of genes plus environment, only the “currently most effective”—which may be superb or less than wonderful, and likely to disappear if a better alternative appears.

Although the idea of selfish genes is simple, a great complexity results. On the one hand, genes can affect more than one trait; on the other, groups of genes can cooperatively affect a single trait. Genes are carried about by individuals, yet genes in one individual may affect the success of genes in other individuals. Some information goes from generation to generation through the cytoplasm, not the genes, and in humans and in some other species, some information is transferred across individuals through culture. Individuals differ genetically, and they live in varied physical and social environments. Thus, while individual strategies for survival and reproduction are all-important, their analysis may be complicated.

We know a great deal about the evolution and ecology of resource use in other species: the costs and benefits; the impact of various environmental conditions; the evolution of sex differences. Genes, history, and environment interact, but the basic patterns are clear. Recent empirical tests suggest that the relative power of chance, selection, and history can differ under various circumstances. Nonetheless, for traits strongly correlated with fitness, even when chance is great in the environment, natural selection is still powerful.

If we humans, like other species, evolved simply to get resources and to survive long enough to get duplicates of our genes into the next generation, why are we so complicated about the process? Even in our life history (chapter 6), we humans are unusual in the pace of our maturation, growth, and reproduction. Socially, we not only live in families (common in many species), but cluster together in villages, cities, nations. We ally ourselves with one another in more
complicated ways than most species, and our groups are based on more than simple reciprocity. We have formal trade agreements and schooling, art galleries, transportation networks, and so on.

This complexity and diversity seem a far cry from any simple set of strategies. Yet despite our complexity, this simple observation is true: those of us alive today are the descendants of those that successfully survived and reproduced in past environments. Historical accidents can happen, but the rules still are true. This means that genetically selfish behaviors, those that enhance an individual’s total genetic representation, are always favored by ordinary natural selection.

Why doesn’t the favoring of genetically selfish behavior always result in bloody outright battles? The short answer is: (1) sometimes it does, (2) when it does not, it is because of the costs of attempting bloody battles. Rules operate under environmental pressures. While all living things have evolved to acquire and use resources to survive and reproduce, the ways they do so are constrained by ecological conditions. Individuals that use the most effective and efficient resource strategies in any particular environment are those that tend to survive and reproduce; but there is no reason to suspect that what works in the desert will work in the river, or that what works among small kin-based societies will work in nation-states. Further, fertility is complex. Although a simplistic interpretation might imply that the best strategy is to produce as many offspring as possible as soon as possible, this is seldom, in fact, a winning strategy even for relatively non-social animals. In some environments, only “superkids” survive and reproduce at all; the result is that fertility responds to the cost of parental investment to make offspring successful. Life history theory is, in fact, largely the study of trade-offs: size against number of offspring, for example. Finally, in social animals, other individuals create some of the most important environmental pressures, and rampant short-term self-interest will often fail (more on this in later chapters). Clearly, rich diversity is likely.

The starting point is that, other things being equal, individuals that use efficient strategies produce more offspring for the next generation than their competitors. But other things are often not equal. Are we sure that we are measuring costs and benefits correctly? At first glance, many behaviors appear counterproductive. For example, infanticide occurs commonly in many species, including lions, ground squirrels, and a number of primates. To determine whether
infanticide is an evolutionary “mistake” or an effective strategy, we must ask: Who commits infanticide, and under what circumstances? Who profits from it? Most infanticide is committed by reproductive competitors; its evolutionary logic seems clear. Sometimes, however, parents kill their own children. How shall we view this? Surely parental infanticide is an evolutionary mistake that decreases, rather than increases, reproductive success? Indeed, evolutionary mistakes are possible. But across species, except for rare pathologies, infanticide is found under specific ecological and social circumstances, and its impact in these circumstances is an increased lineage success for the killer—even when the killer is a parent.  

How can this be? In species in which a successful offspring requires considerable parental effort, there are circumstances in which terminating a particular investment pays off—for example, a deformed offspring or a mother’s poor health. In these circumstances, parents win who discriminate by investing more in offspring that are more likely to be successful, and investing less in weak or deformed offspring—even in the extreme case of infanticide. Other similar puzzles of apparently maladaptive, yet common, behaviors include lethal conflict (when does it pay to risk getting killed?), delayed reproduction (how can waiting to reproduce increase one’s reproductive success?), and sterility (the ultimate in nonreproduction).  

Consider honeybees, in which all females except the queen are sterile. How can a (female) worker bee’s genetic representation possibly be increased by remaining sterile and devoting her life to caring for the queen’s, her sister’s, eggs?  

Darwin worried about how a trait like sterility could be inherited. He understood that honeybee colonies were somehow special, but left the solution for future researchers.  

Perhaps the most blatant examples of hard-to-explain phenomena fall under the heading Darwin called “sexual selection.” He understood that anything that helped you survive would be “favored,” but unless you also reproduced, that trait would disappear. The reason Darwin treated sexual selection separately from “ordinary” natural selection was that successful sexual strategies in so many species were also dangerous, life-threatening strategies, usually associated with male-male competition. Darwin struggled to understand how such behaviors could be favored by selection. It took much observation to determine that (1) sometimes the most effective thing you can do is take a huge risk, and (2) in a sexual species, reproducing means that you must face both the competitors of your own sex and the
preferences of the opposite sex you wish to win. So, Darwin argued, others of your species could “select” just as effectively as the horse or cattle breeders who change the genetics of future race horses and milk cows by selecting who gets to breed. Sex differences, how they arose, and how and when they are maintained are at the heart of my exploration, and I will return to these themes repeatedly.

**Whose Genes Count, and Why? Kin Selection**

Though the concept of selfish genes is a simple one, it has been repeatedly misinterpreted, just like Darwin’s original formulation. How horrible, “Nature red in tooth and claw”! How could we possibly believe such a noxious idea, when we can see generosity all about us in many species. It remained for biologist W. D. Hamilton to quantify and formalize some of the most important genetic costs and benefits of behavior—and his formula, though simple, is to much of biology what \( E = mc^2 \) is to physics.

The first general rule is that a behavior will become common only if its genetic benefits outweigh its costs—if \( b > c \). Hamilton pointed out that, since “nondescendant” relatives of any individual ("ego") such as nieces, nephews, and siblings share genes with ego, helping these relatives (even if it has a direct cost to ego) can help ego’s genes. To be favored, there must be a net genetic benefit. Relatives shares only some genes with the helper, and this varies with \( r \), the degree of relatedness; your sister has more genes (higher \( r \)) in common with you than your fifth cousin. So the benefit must be discounted, and only the help that goes to identical genes counts. Hamilton pointed out that “giving” behavior should evolve whenever \( rb > c \), that is, whenever the benefit to the recipient \( b \) times the degree of relatedness \( r \) is greater than the cost to the doer—for example, whenever the benefit to one’s sibling, who shares on average one-half of one’s genes, exceeds twice the cost of one’s act, or when the benefit to each of two siblings exceeds the cost of the act.\(^{11}\) Notice that this also means that not all help to kin will be favored: if the cost to self exceeds the (benefit \* relatedness of kin), the behavior should disappear. And sometimes being positively mean to one’s kin pays—when \( b_{self} > r_{rel} c \) (simply reorganizing the above).

This concept had been recognized informally for some time. The mathematical biologist Haldane had noted that, while he would not
give his life to save his brother (who would, on average, share half his genes), he would die for two brothers, or eight cousins. Hamilton applied this concept of inclusive fitness maximization or kin selection to Darwin’s puzzling problem of sterile castes in social insects (surely it is a great sacrifice not to reproduce and spend one’s life caring for a relative’s offspring). He could show why Darwin was correct in maintaining that the self-sacrificial behavior persisted only because it occurred in the familial context, and that it would not persist in other sorts of groups.

The point is that a behavior can be genetically profitable even if, to the casual observer, it appears to be costly and of benefit to others (table 2.1). This distinction between what seems to be true and what a behavior does for relative genetic representation is a thorny one, but one we cannot ignore. Measuring both costs and benefits correctly is crucial.

How many genes we are likely to share with another individual (r, the degree of relatedness) is one key to how much we will profit

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<th>Behavior</th>
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<td>Overt competition</td>
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<td>Parenting, nepotism, reciprocity</td>
<td>Costly (“altruistic”)</td>
<td>Profitable (“selfish”)</td>
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Because natural selection favors only genetically profitable behaviors, under natural selection behaviors above this box should be common; below the box, rare.

??                                 | Profitable (“selfish”) | Costly (“altruistic”) |
Mother Teresa?                     | Costly (“altruistic”)  | Costly (“altruistic”)                  |

Notes: If we look only at superficial, apparent (“phenotypic”) impact, we miss crucial differences. ?? = this category is so very rare that I have trouble imagining a non-controversial example: Perhaps a rich miser (phenotypically selfish, since he is a miser) who disinherits his family, leaving an anonymous gift to a home for unwed mothers (genetically altruistic, since he hurts his relatives in order to help genes, not IBD). See chapters 9 and 10 for further exploration.
by helping. As humans, we are likely to have, on average, half of our genes in common with a sister or brother. All adult humans have two alleles at each locus, or location, on every chromosome (with some special conditions for the X and Y sex chromosomes); these two alleles can be duplicates (homozygous; perhaps both are the allele we call $a$), or different (heterozygous, perhaps $a$ and $A$). We received one set from our father, one set from our mother. Mother’s egg and father’s sperm are produced in a lotterylike process called meiosis; each resultant egg or sperm has only one set of chromosomes. An egg or sperm has some chance of getting either allele at any location. Suppose my mother is heterozygous, and has $aA$ at the locus I am interested in. My sister and I might both receive an $a$ or $A$ from Mom, or one of us might have $a$ and the other $A$ (and be totally different in what we inherited from Mom). This pattern is true for each genetic location, and true for what we received from our mother and our father. As a result, we share about one-half of our genes with our full sister, and one-fourth of our genes with her child (fig. 2.1). Your own child, of course, shares exactly half your genes.

Hamilton suggested that striking phenomena follow from the fact that social insects have the peculiar genetic arrangement in which mothers produce sons by laying unfertilized eggs. Because males have no father and get only one set of alleles from their mother, they have and pass on exactly the same genetic material in each sperm. So in social insects like honeybees, full sisters share identical genes through their father. They can never be less than one-half alike if they have the same father, and they are more closely related to each other on average ($3/4$) than mothers are to daughters ($1/2$). Sterile female workers, Hamilton suggested, were not paying, but gaining, genetically by raising their three-fourths-alike sisters rather than half-alike daughters. While this hypothesis may not fully explain eusociality, Hamilton’s statement of the theory of kin selection was more general and is an important part of the general theory of natural selection. Hamilton’s summary hypothesis makes a strong, testable prediction: “The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbor’s fitness against his own according to the coefficients of relationship appropriate to that situation.”

Thus, other things being equal, we expect individuals to treat their kin more gently than strangers, and to treat close kin more gently than distant kin. Even though we expect no organism to be able to
Figure 2.1. Hamilton's (1964) theory of inclusive fitness maximization suggests that behavior will evolve as a result of its costs and benefits not only directly to the doer, but on those to whom the behavior is directed, depending on the degree of relatedness. Helping behavior will be favored as it helps more genes that are identical by descent, and less favored as its effects are diluted by genes that are not identical; thus the proportion of shared genes is important to calculate. Here, Ego (5) receives half her genes from her father (1) and half from her mother (2). Her daughter (10) receives half her genes from Ego. Because her brother (4) is a full sibling, with the same mother and father, he will, on average, be genetically half identical to Ego; his daughter (9) will be exactly one-half like him, and on average, one-quarter like Ego. Individuals 3, 8, and 11 (relatives of Ego's mate) share no genes that are identical by descent. (From Williams 1992a)

calculate its relatedness to others, we expect them to act as though they could. In fact, of course, what we see is that organisms treat those with whom they grow up differently from others, because under most circumstances in most species, individuals grow up among relatives, not strangers. Hamilton describes an individual's strategy for making effective use of proximate cues of relatedness.15

In many species this proximate cue of nearness works because the individuals with whom one grows up typically are one's relatives. This is why, for example, a researcher can fool ground squirrel mothers into adopting unrelated babies before her own children emerge from the nest to forage above ground, but not after, when there is opportunity for mothers to make costly mistakes, as youngsters occasionally blunder down the wrong burrow. Research on a wide variety of species has so far supported Hamilton's prediction.16 Each individual has reproductive interests, but these interests are shared to a predictable degree by others who also share common genes—genes identical by descent. Overtly selfish behavior, "nature red in
tooth and claw," is thus only one route to enhanced genetic representation (table 2.1, fig. 2.1). Individually risky or energetically costly behaviors and helping one's kin can also be genetically profitable. We expect organisms, including humans, frequently to engage in activities that benefit relatives. Further, highly selfish behaviors will not be genetically profitable in the longer run if they harm relatives too much.\textsuperscript{17} Human history has a wealth of examples: the impact of family on death rates in crisis situations, alliances and internecine warfare in Icelandic and English history, and others.\textsuperscript{18}

How much relatives profit from helping or harming one another will depend on the degree of relatedness as well as on the costs and benefits of the act. Helping relatives, even at some cost to oneself—and helping friends who will reciprocate, for example—can be genetically profitable, and many behaviors that appear to cost the performer are actually profitable in terms of genetic representation. Here, it is the actual effect on reproduction and genes that we care about. Reciprocal coalitions can be complex and quite elaborate in humans (think of politics, and of warfare), and they affect men and women differently; I will return to them in chapters 10–14.

**Summing up the Basics: Assumptions and Objections**

The forces of selection, including kin selection, explain much of the variation in the behavior of individuals in other species. To ignore them completely when it comes to humans would be absurd. Imagine how much credence you would give to me if I told you that gravity exists, making all other animals behave in certain ways (walking on the ground, being able to glide only a short distance, or expending considerable effort to fly), and then went on to explain that humans, on the other hand, are exempt because we have cultural phenomena such as airplanes. We have more complexity and more variation in how we can travel on the ground or in the water, and because of our cultural transmission and elaboration (including inventing and sharing technology), we are not bound to the ground; we can clearly fly in ways unknown among other species. And when we fly, it is because of our cultural innovations and personal desires, not because we "need" to. Nonetheless, you would probably still bet that gravity influences all of our travel. While we can circumvent
gravity in sophisticated ways, it never disappears as a force to be reckoned with.

This is not the place for a lengthy review of behavioral basics; some excellent reviews already exist. But because the behavioral outcomes I explore here involve not only rules but environments and history, I want to be explicit about what I am, and am not, suggesting about our human sex differences. Behavioral ecology asks whether, if we know about environmental conditions (including social conditions) and how those conditions change actors' (genetic) costs and benefits, we can predict the kinds of behavior we are likely to see. To explore this possibility requires assumptions. These include the following:

1. Organisms are generally well suited to the environments in which they live; they achieve success in any environment by getting resources that enhance their survival and reproduction. Strategies we see have had time to compete against other strategies, and "what you see is what you get" — it is what has worked best (the phenotypic gambit).

2. Only heritable variation is appropriately considered in testing predictions about changes in gene frequencies over time. An individual can assist its genes to spread
   a. by reproduction, the most direct method; or
   b. by assisting individuals carrying copies, identical by descent, of its genes (kin selection); or by helping individuals that do not carry identical copies of its genes, if such assistance is returned in genetically effective ways (reciprocity).

   This implies that individuals who help reproductive competitors without any reciprocation will lose descendant representation in existing lineages. In short, people like them will become rare or cease to occur.

3. Organisms that are more efficient in getting resources in any environment will survive and reproduce better than others. In the evolutionary history of all species, there have been important proximate correlates of reproductive success, including resources (food, territory), rank (status or power), wealth, and, in highly social species such as humans, social "reputation."

4. Further, no organism, including humans, has evolved to perceive or assess directly the spread of genes; rather, organisms behave as though these proximate correlates were their goal. Thus, species
may find themselves in novel evolutionary environments, and individuals’ behavior may be currently maladaptive; when this is true, the assumption of the phenotypic gambit is violated.

5. In their “deep” objectives—in what they evolved to do—humans are not qualitatively different from other living organisms. Like other living things, they evolved to get and use resources to survive and enhance the spread of their genes. To evolutionary biologists, this is parallel to arguing that humans, while they can make airplanes and fly, for example, are still subject to the laws of gravity. Yet because they are highly intelligent and highly social, humans are the likeliest of species to be in novel environments, making it a complex task to make assumption 4, and to distinguish evolutionary history from current utility.  

Perhaps because the study of human social and sexual behavior has in the past “belonged” to fields in which only humans were studied, this is a novel approach. A behavioral ecologist would answer the query, “How do I love thee? Let me count the ways,” far less poetically than Elizabeth Barrett Browning. For several reasons, this approach may not be palatable to all. It may also be controversial; certain assumptions are simply not accepted by everyone. Many think, for example, that it is inappropriate to use the same general principles to examine human behavior as to study the behavior of other species, even to test hypotheses; and many feel that not all behaviors can be reasonably analyzed.

A widely held discomfort with any evolutionary approach to human behavior is the one reflected in the following (perhaps apocryphal) story, which I first heard attributed to Bishop Wilberforce’s wife. When Darwin presented his theory of natural selection, hers was a typical response as she leaned over to say to her friend, “My dear, have you heard Mr. Darwin’s theory that we are all descended from apes? Let us hope that this not be true; and, if true, let us hope that it not become generally known.” It is easy to agree with the bishop’s wife, or to fear that knowledge of behavioral ecology will lead us to make bad or cynical policy. This confusion of “is” and “ought” is sometimes called the “naturalistic fallacy.” Because evolution is simply genetic change over time and thus amoral, its analysis is analytic rather than normative, and it has no bearing on human moral decisions. To observe that something is true does not constitute a moral endorsement.
Human complexity and flexibility raise special analytic concerns. Simply because a trait looks useful, we cannot assume that it evolved through the action of selection. It is important to articulate the proposition one is using to generate hypotheses, and to state one’s assumptions.\(^{23}\)

In relatively stable environments, we expect selective pressures to remain similar over time. Thus, for example, constant cold leads to stumpy limbs and cold-tolerant physiology. This does not mean that any particular observation can offer strong support; the camel’s hump, for example, might have come about for nonselective reasons, because of natural selection, or due to some combination; and humans are a particularly difficult entity to study. But if we accumulate a series of a priori predictions, they can grow into a significant number of directional results. In other species, special insulating hair and feathers, found in numerous species—but only in Arctic and Antarctic environments—suggest selection. For complex phenomena in complex species, such as social and sexual behavior in humans, this teasing apart is an issue to which we must pay careful attention.

What about exceptions, what a colleague of mine calls the “Bongo Bongo” argument? “This is how the world works, and you can see I’m right, for among the Bongo Bongo they . . . .” Or the reverse: “Your view of how the world works is obviously wrong, for among the Bongo Bongo, they are absolutely altruistic to everyone.” Or: “Gravity cannot be a natural force, for birds and humans can fly.” Hardly persuasive. Behavioral ecological predictions are statistical, arguing that at any moment, behaviors that, in a particular environment, get genes passed on will increase relative to other behaviors, and that (employing the phenotypic gambit, and statistics) we are likely to be able to detect this trend. Thus, if we find that the Bongo Bongos are truly genetically altruistic, this means only that the Bongo Bongo are likely to decline over time, to be replaced by competing peoples—and this is a testable prediction.

All of the arguments in this book, in the context of natural selection, are statistical propositions that, other things being equal, individuals with certain traits will be, or will become, more common than competitors in particular environments. None is a statement of absolutes. Consider: Many people would consider Mother Theresa a genetic altruist, helping nonrelatives for no genetic payback. If I argue that genetic selfishness is favored, I am not suggesting that we will never have a Mother Theresa—only that, over time, her genetic
lineage will likely decrease compared to others, and she and others who are genetically altruistic will remain a rarity. We are making predictions about what a statistician would call “central tendencies” rather than rare exceptions.

**Novel Evolutionary Environments: Can the Principles Still Hold?**

A very large question remains: How far can we usefully explore our current behavior? Environments that are new and novel in an evolutionary sense introduce significant complexity. After all, it might be easy to see how reciprocity and discrimination are favored in people living in small bands, interacting daily with the same few people, and protecting some resource against outsiders. But today our societies are large and complex. We may interact with literally hundreds of people; we do business daily with people we have never seen before; we have information about what happened today across the world, to strangers we may never see. History also complicates our problem: we know of many nonselective accidents in our history that are equal to the destruction of Pompeii.

Novelty poses a great difficulty for studying human behavior; through our cleverness, we constantly create environments that are novel in selectively important ways for ourselves and other species. The behaviors that helped hunter-gatherers in the savanna may not be useful in the suburbs of Chicago.

Novel evolutionary events influence behavior and demography of other animals as well as humans. For example, a male chimpanzee in a well-studied group gained dominance status by banging together empty metal containers instead of the more traditional branches. In Great Britain, Great Tits began to feed out of milk bottles that were evolutionarily novel, although the bird’s probing behaviors had evolved to forage on bark and twigs and their digestive systems certainly did not evolve to deal with milk. On the East Coast of the United States, gulls, evolved as generalist feeders, showed marked increases in population density as a result of an increase in garbage dumps, while other seabirds declined in abundance due to gull predation. Consider the Arctic fish discussed in chapter 1: because the water has, for millennia, been just above freezing, there are several Arctic fish species in which one can kill an individual—
through heat stress—just by warming it up to temperatures we would still find frigid. However, if global warming continues, the water in some areas will become warmer, and whether any fish in a particular species still retain the genes for warmth tolerance is a toss-up. For the Arctic fish, over many fish generations, cold tolerance was profitable, and ability to tolerate warmth was not. But now we are changing the environment.

The impact of novel environments is heightened by the fact that no organism, including humans, has evolved to be aware of ultimate selective effects, but only of proximate cues. Selection acts in a way that what enhances our survivorship or reproduction—forming friendships, having sex—tends to be perceived as pleasurable; and acts that typically detract from our survivorship or reproduction—for example, getting burned—are unpleasant or painful. But this relationship can change when the environment changes. Consider a simple example of novelty. In nature, sweet foods are seldom harmful, and sour and bitter tastes are often correlated with the presence of harmful alkaloids. Thus a preference for sweet tastes (a good proximate cue to nutrient-rich, safe food) became widespread in omnivores, including humans. In most past environments, it was difficult to obtain enough sugar to create problems of obesity. Once we humans invented technologies for refining and concentrating sugar, we created foods that had enormous concentrations of sugar, breaking the selective link between sweet taste, the proximate cue, and good food source that had previously led to enhanced survivorship and reproduction. But proximate cues drive the system, and selection acts as a passive sieve. So we retain a preference for the sweet taste that can make us fat and fill our teeth with cavities.

Because we humans can modify our environments so extensively, and because our cultural transmission can respond more quickly than genetic intergenerational transmission, we are frequently in novel environments. It is surely fair to ask how far we can really expect to see selectively advantageous behavior in our current environments. As an example, consider the following: In other species, and in preindustrial human societies for which we have data, males who have more resources typically have more offspring (usually because they have more mates) than others (chapters 4, 7, 8). Now, in much of the world, effective contraception has broken the link between resource accumulation and fertility (the Pill is so extraordinary that The Economist recently included it in a list of the Seven
Modern Wonders of the World). For the first time in all of history, men and women could be on equal sexual footing; sex could be without parental consequences for either. Certainly this is a novel environment. But we humans, like other species, operate on proximate cues, not any awareness of selection; the existence of the Pill, breaking the link between sexual pleasure and parenthood, doesn’t mean that sex is no longer fun. So do wealthier men today, as in the past, have more children than others? As I explain in chapter 15, possibly not, because of the novel environment. But they do have more sex, if they want it.  

MORE THAN ANTS OR PEACOCKS: LIFETIMES, CULTURE, ECOLOGY, AND VARIATION

My explanation of the basics of selfish genes does not yet come close to being useful in looking at human behavior in all its diversity and complexity. Three important ingredients remain to join in the interplay: the social impacts of sexual reproduction (chapters 3–5) and how these play out in human lifetimes (chapter 6); the influence of external environmental influences (chapters 7, 8); and the intense pressures of group living (social influences), which elaborate reciprocity as a social force beyond anything we see in other species (chapters 9 and 10).

Three phenomena—kin selection, reciprocity, and sexual selection, or how we interact with family, friends, and mates—lie at the heart of why we behave as we do in many circumstances. The basics give us a perspective on complex phenomena, and I will try to weave together the themes of the ecology of resource consumption and sex differences in different ecological situations. My central task here is to ask why we behave as we do, especially about resource issues, and why the sexes differ so consistently in some areas, and not at all in others.

I began by assuming that we humans share some constraints with other animals (and plants, too, for that matter): we must get resources to survive and reproduce; parents and offspring are more like each other than like strangers; and what is effective in one environment won’t necessarily work in another. Although only heritable variation is important, in complex social animals like ourselves, cultural transmission is one kind of heritability, and interaction be-
tween cultural and genetic transmission can certainly complicate analysis (chapter 10).

The advantage to this approach is that we can frame questions in ways that have some rigor and repeatability. That is, we can go beyond convenient “Just So” stories such as “How the Camel Got Its Hump” or what causes vampires. It’s not easy; in its crudest formulation, natural selection theory sounds like a circular argument (what works, works, so if you see it, it must be working). Of course, so do the principles of physics. We also are tackling complex and interrelated phenomena. The trick is to figure out for what traits we wish to predict the direction, along with what environmental forces we predict will favor this versus that version of the trait. Then we can predict the direction before we go out to measure it: “If the environment is A, then version X of our trait should increase over time; if the environment is B, version Y should increase.” Then, if we see what we expect, we have support (but not proof) that we are likely to be at least partially right; and we know that if we see something else (e.g., version Y runs riot in environment A), we must be wrong or else there is a factor missing from our analysis.

The philosopher Helena Cronin developed the apt imagery of the “ant and the peacock” to suggest how kin selection (ants) and sexual selection (peacocks) influence the lives of living things. I wish to explore here not only the similar ways in which selection has acted on us (to what extent we are all ants and peacocks), but also the specific ways in which conditions in the external environment are good predictors of differences in the ways men and women approach resources. Finally, I will discuss the reproductive impacts of today’s evolutionarily novel environment.