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Introduction

Probably a crab would be filled with a sense of personal outrage if it could hear us class it without ado or apology as a crustacean, and thus dispose of it. "I am no such thing," it would say: "I am MYSELF, MYSELF alone."

—William James *Varieties of Religious Experience* (1902)

To the same natural effects we must, as far as possible, assign the same causes.

—Newton

“WHY CAN’T A WOMAN be more like a man?” wailed Professor Henry Higgins in *My Fair Lady*, the musical derived from George Bernard Shaw’s *Pygmalion*. Certainly in many societies, across time, there have been women who were “more like a man.” Think of Joan of Arc, who was burned at the stake (on the minor charge of wearing men’s clothing); or of George Sand, of whom Elizabeth Browning said, “You are such a large-brained woman and a large-hearted man.” Yet in part, we remember such women *because* they are singular, whether we envy their ability to break free or whether we imagine that they missed a lot. What really contributes to the patterns we see—and to their exceptions?

Here I want to explore sex differences from a relatively unusual perspective, one that is often misunderstood. Understanding and explaining human behavior is a central concern for all of us. But doing so—especially when sex differences are the issue—presents a real dilemma. We are complicated, highly social beings. We live in a staggering array of environments, both ecological and social. Our families, lovers, and friends are not exemplars or prototypes, but unique, particular individuals. None of us wants to be “reduced” to some formula.

For, like William James’s crab, we *know* we are above crude analysis. Even the name we give ourselves, *Homo sapiens*, reflects both the value that we give to understanding and the fact that we feel ourselves to be special. Like that crab, many people may be appalled at the approach I will use here, that is, to assume that, once we understand environmental and social pressures, we humans are

as predictable as other animals in our behavior and are governed by the same rules. And I want to begin with *simple* rules, no less.

Many of us assume that humans operate under rules that are different from these other species, that our rules are based entirely on culture rather than on biology, or some combination. I will ask: what can we learn if we begin without assuming that this were true? I want to begin by exploring what a biologist would predict if he or she knew only that here was a smart, upright-walking, highly social primate and *nothing more*. I will explore the ecology of being male and female, beginning with simple rules and with what I can discern about the environments with which the evolutionary rules interact.

The approach I use, behavioral ecology, is an evolutionary approach with roots in Charles Darwin's work. It focuses on the question, how do environmental conditions influence our behavior and our lifetimes? This approach has proved profitable in exploring other realms of human behaviors.¹ Behavioral ecology and its intellectual relatives seek to understand how comparatively simple operating rules interact with historical accidents, and with temporal and spatial specifics, to yield a rich diversity of patterns. There is no doubt that genes influence not only our physical structure and physiology but also our behavior; there is no doubt that historical accident often plays a role, nor is there any doubt that cultural and social pressures can influence behavior. But where lies the balance? Perhaps by beginning with very simple rules and assumptions, and finding where they fail to predict well, we can gain some insight.²

VAMPIRE STORIES AND BEYOND

Humans have always sought to explain the patterns they see. In fact, one of the strongest selective forces on human behavior has been to understand pattern—not only in order to deal with environmental variation but also to be the first in one's tribe who is able to predict events and when they will occur (imagine being the first human to predict a solar eclipse). But creating stories that more or less match our observations is not science but folklore.

Consider vampires. From Bram Stoker through Anne Rice, from Bela Lugosi to Tom Cruise and Leslie Nielsen, vampires have always fascinated us: aristocratic, sexy, dangerous, and (almost) invincible. Vampire folklore provides a wonderful example of how our need to explain can drive us to spin stories that *seem* to explain something that we see, and that can be hard to refute, but that nonetheless do not reflect what actually happens.

The folklorist Paul Barber, in a delightful examination of vampire myths around the world, notes that the ways people in preindustrial societies interpreted phenomena associated with death and the decay of corpses are “from our perspective, quite wrong. What makes them interesting, however, is that

they are also usually coherent, cover all the data, and provide the rationale for some common practices that seem, at first, to be inexplicable.”³

The variety of myths and legends about vampires all begin simply: death—especially unexpected or unusual death—brings more death. If someone died, “why” was usually unknown, and epidemics leading to death and more death were once far more common than today. Once people were buried (often without coffins), not all corpses had the decency to stay below ground. In a prebacteriology culture, people weren’t likely to see a “flailing” corpse as the natural by-product of bacterial decay, but rather as the will of the dead person or as the rejection of the corpse by Mother Earth. Since death brings death, those first to die, as in an epidemic, were dangerous and somehow had to be disarmed so that they could not continue to bring death. Only when all “changing” ceased, and ashes or bones alone remained, was the corpse neutral, inactive, and no longer dangerous.

People thus began with a repeatable observation: that death brings death. This applies not only to vampires but also to the general idea that dead people call to their relatives and friends and must be propitiated to protect those still alive. Because they had no knowledge of disease transmission, people imbued the corpse with dangerous properties. Not a bad idea, particularly in times of plague, when unexpected deaths were frequent and vampire fears were heightened—but an idea that led to a misinterpretation of the normal signs of decomposition.

In folklore, in a variety of societies around the world, vampires are described as undecomposed; they have a ruddy or dark complexion, do not suffer rigor mortis, are swollen or plump, have blood at the mouth and/or in internal cavities, and grow new skin or nails after burial. In an interesting twist, people suspected of being vampires were frequently buried differently, in ways that made a diagnosis of vampirism *more*, not less, likely. Suspected vampires were often buried face down, so that if they tried to claw their way out of the earth to torment others, they would dig themselves in deeper. But because blood settles into the lowest capillaries after death, face-down burial meant that the body’s face (rather than the back) would be dark and ruddy. And a ruddy face was believed to be a sign of a vampire. Some putative vampires were buried with lime to hasten their decomposition—but lime in fact retards it. Thus, someone who died in an unusual way and was in danger of becoming a vampire was likely to be buried face down, covered with lime—and thus to have a ruddy face, to decompose more slowly, and, on exhumation, to be confirmed as a vampire. Such practices reinforced mistaken beliefs.

Folklore about vampires arises from an entirely sensible and consistent desire to explain something in the absence of complete information. But what people *say* about what they see and do can be a rotten path to explanation. Although observers called the corpses undecomposed, they described unmistakable signs of rot (e.g., a stench). Descriptions like “ruddy” or “swollen,” which

were used to assert failure to decompose, are in fact signs of the ordinary (but variable) process of decomposition.

It is important to separate carefully what people *describe*, as they see, hear, and smell what happens, from the *causes they attribute*. The observation that a corpse stinks is, in fact, consistent with the contention that decay is occurring, but not that it is failing to decompose. It is important to avoid this kind of muddle at all times, not only when we are no longer likely to believe in something like vampirism. Being led astray by “vampire myths” that sound reasonable but are untested is most likely to occur when a behavior is complicated and we want to believe the stories we tell.

EXPLAINING BEHAVIOR WITHOUT FOLKLORE

Other species' behavior can be more complex than we realize. An excellent example of such complexity generated by the interaction of operating rules (genes), environment, and historical accident is the biologist Bernd Heinrich's work on food sharing in ravens, *Corvus corax*. Heinrich saw a curious behavior on a hike in Maine late one October: a group of ravens that were feasting on a dead moose were giving a distinctive, loud, and high-pitched “yell.”⁴ Because other ravens were attracted to the yelling, the result was that there were more competitors at the kill, and thus less food for each of the yellers. Why didn't the raven who first found the kill just keep quiet? And why weren't the ravens now fighting over the kill?

If we saw humans share like this, or if we extended our often untested social perceptions about humans to ravens, we would probably think how kind all this indiscriminate sharing is. In fact, that would constitute a vampire story; behavioral ecologists find true genetically costly altruism to be so rare, as I will explain below, as to be a fluke in nonhumans. The ravens who shared seemed to be doing it at a cost. One of Heinrich's first questions was whether the “called” birds were related to the callers, for sharing with individuals who have at least some genes in common can help copies of one's own genes. Or were they reciprocators? After much work marking and recapturing ravens in the field, Heinrich was able to eliminate the possibility that ravens were summoning their kin or their reciprocators. Where next?

Heinrich made a series of careful observations, comparing the behavior of different ravens under different circumstances. His summary begins with eleven clues and proceeds from simpler to more complex deductions.⁵ Without giving away the whole plot, I can say that one of his major findings was that *adult* ravens are territorial, controlling access to any carcasses in their territory and driving off any juveniles found on a carcass. When a *juvenile* found a carcass, it was likely to “yell,” attracting other juveniles (the largest group at a carcass was about 150). When enough juveniles were present, the resident territorial adults

could not drive all of them off. So the cost of additional juvenile competitors could be offset by the benefit of attracting a group large enough to stay on the carcass even if adults were nearby. Clearly the costs and benefits of yelling would vary in different circumstances. Heinrich did not simply create a plausible vampire or just-so story about the juvenile behavior he observed. Instead, he observed, made hypotheses, and tested them to discover the most probable functional reason for the ravens' behavior.

Heinrich could not know what role any gene plays in this behavior, so he used a technique called the "phenotypic gambit" to make testable predictions: starting from what he saw—the phenotype—he made certain assumptions. He assumed that, whatever the relationship between genes and the set of behaviors he saw, enough time had passed for the system to come to equilibrium and thus what he saw represented the outcome of competing strategies.⁶ The phenotypic gambit is a powerful tool (although sometimes controversial), and I'll return to it below.

For ravens as for humans, both ecological and social conditions can change the costs and benefits of any action. Heinrich, of course, had to observe the ravens without their cooperation; he had to concentrate on what the ravens actually did. Sociologists, psychologists, and anthropologists find it useful to interview people, and this tells us something about what people themselves imagine they are doing (and, of course, speech itself is a behavior).

Because we can make decisions consciously, often we assume that unless a behavior is consciously considered, it is of no interest. Yet many other species routinely learn and behave in complicated ways without (so far as we can tell, at least) consciousness—or at least without the ability to share abstract sentiment through speech. Furthermore, as I noted above, it is presumptuous to assume that people's conscious attributions of their behavior are analytically helpful, and if we do assume that, it can cause real trouble.

Behavioral ecologists cannot interview ravens about why they call to other ravens when they find a carcass (who knows what reasons a raven might give, anyway?), and they don't know the genetics of the situation (is such calling the result of a single gene's action?). For these reasons, behavioral ecologists concentrate on what happens—on what behaviors show up under what conditions. If we take the same approach in looking at human behavior, we will lose some information about people's intentions, but we won't get distracted by our human reports of conscious reasons. And such lack of distraction may prove useful, for what people say is often not consistent with what we observe them doing.⁷

Perhaps new connections will appear as we look past what we imagine behavioral causes to be and as we look beyond what people say about why they act a certain way—if we instead examine carefully *what sorts of behaviors we see in particular environments*. Without requiring consciousness or rationality (or even speculating on their existence), we can ask what behaviors will be profitable under specific environmental conditions. Then we can ask explicitly

how conscious, cultural influences can influence the costs and benefits of these behaviors.

KINDS OF “WHY” QUESTIONS

Heinrich’s analysis of raven behavior highlights an important distinction. To understand “why” we do things, to explain both the behaviors that seem almost universal or unvarying and those that vary greatly, we can seek answers in different ways. “Why” questions have two principal complementary forms in biology: “proximate” and “ultimate” explanations.⁸ Why do birds migrate? One answer might be “changing day length causes hormonal changes, triggering migration.” Both changing day length and changing hormones are *proximate* triggers, or cues. If we could interview birds, we might have another set of proximate causes, the equivalent of our reasons: “I really hate the cold,” “it makes me feel good,” “that way I get to see my relatives.”

However, proximate answers are no help in explaining why one species migrates while others don’t, why not all individuals in this species migrate (costs and benefits may differ for older, younger, weak, or healthy individuals), or why day length rather than some other cue, or a combination of cues, has become the trigger.

The *ultimate* cause of migration (and other behaviors) always concerns reproductive success. Seasonal better-versus-worse geographic shifts in foraging and nesting areas mean that individuals who seek the better areas, shifting seasonally, leave more descendants than those who remain in one area. When day length is the most reliable predictor of these seasonal shifts, individuals who use it as a cue will fare better than those that use some other proximate cue or who fail to migrate. Thus, we would predict migration patterns triggered by day length for birds that are (for example) insectivores or nectar-eaters in northern temperate regions; their food disappears seasonally. We expect variation in which individuals will migrate when: the benefits and costs of migration (in terms of survival and reproduction) differ for older, prime-age birds compared with yearlings in a particular species, for example. Proximate cues and ultimate (selective) causes tell us very different things.

It is useful to ask questions about both “proximate” triggers and the “ultimate” selective cause, and it is important to understand that these two approaches are not alternatives but that they complement each other. Proximate triggers, the *mechanisms that release behaviors*, are sometimes also called “causes.” They tell us what kinds of environmental factors are reliable. The ultimate cause of a behavior’s existence, in evolutionary terms, is always its impact on family (or genetic lineage) persistence through time. We seldom think of such matters, perhaps because few of us can now trace our ancestry in the same way a certain schoolteacher from Cheddar, England could: a preserved “bog man” from an-

cient times was found, through DNA analyses, to be a clear direct ancestor of his.⁹ Nonetheless, the persistence of genes through time, and the clustering of genes in family lines, are real.

Sometimes it is important to ask “why” at the proximate level. Suppose we wish to ask about variation in human fertility. Reduced fertility could have the proximate “cause” of later marriage age and an ultimate selective cause of greater lineage success through fewer, better-invested children than through more numerous, but less able, children. We humans would naturally think about the first of these, but seldom about the second.

We could interview people about their conscious reproductive decisions, the proximate causes. If you were interested in manipulating what people will do, this would be the appropriate level at which to ask the question.

Behavioral ecology, in contrast, seeks to discover which behaviors in which particular environments result in greater success (more about definitions of success in a moment). It starts with a bias toward “ultimate” questions, although it seldom can ignore proximate correlates. We can profit from disaggregating—teasing apart—behavior patterns in a population: who does what, under what circumstances. Consider the following: we might discover that, in a particular society, men who marry younger women have more children over their lifetimes than men who marry older women; we would not then be surprised to find a “proximate” social preference for youth in wives, nor would we be terribly surprised to find that older wealthy men in this society marry younger women more often than do poor men. The behavioral ecologist is more interested in the first question: Does marrying a young wife affect a man’s lifetime reproduction? A cultural anthropologist, on the other hand, would be more interested in the ways women and men make marital decisions in this society.

Answers to both kinds of “why” questions are informative. And certainly any human society can make decisions to foster behaviors that are counterproductive in terms of ordinary natural selection, though no proximate “cause” is likely to remain common for more than a few generations if it does not serve an ultimate selective cause. For example, the Shakers are a religious group that imposes celibacy on all its members. That’s certainly a cultural rule with biological implications: the few (perhaps three?) Shakers remaining today are not being replaced.

Proximate mechanisms can enrich our understanding. The usefulness of specific mechanisms depends on (1) what best predicts important changes in the external environment and (2) what internal devices already exist in the organism. When our primary concern is intervention (as in medicine or family planning), these particulars of proximate mechanisms become important. To understand the ultimate evolutionary purpose, we are more likely to study the correlations between organismal traits and environmental conditions. For example, when predictably timed periods of very cold weather alternate with food-rich moderate-temperature times, we expect trees to lose leaves (to conserve water), nectar-eating birds to migrate, and so forth.

SIMPLE RULES, COMPLEX OUTCOMES

Although humans are more complicated than other species in many ways, the exercise of asking questions in the same way about ourselves as we do about other animals may be instructive for two reasons. First, other species, like ravens, are often more complex than we realize—and we learn much from studying their behavior. Second, even as we tout our human complexity, we have sometimes offered remarkably simplistic explanations about human culture and behavior. Recent work applying the same standards of repeatability and hypothesis testing to our own behavior as we do to that of other species suggests that we can gain important new insights.¹⁰

My explorations here assume that humans are indeed animals, even if elegantly complex ones, and that they are therefore subject without special exemption to the general rules of natural selection, the rules that govern behavior and life history among living things. We are still exploring the gene-behavior links that are likely to be important, but it is nonetheless clear already that genes are a “currency” to be maximized in various behavioral equations. We can explore to see what we can learn about human behavioral patterns by considering genes alongside more standard currencies like status or money. The philosophy of keeping underlying assumptions as simple as possible is sometimes called “Occam’s razor” in the sciences. To paraphrase Einstein, “Keep things as simple as possible, but no simpler.” That is, seek the simplest model that captures the important patterns, whether the model is verbal or formal. Then, step by step, add real-world complexities to the model.¹¹

HUMANS AS CRITTERS

Despite our cultural complexity, we humans must solve the same ecological problems as all other organisms in order to survive and to reproduce. That is, in any environment, individuals must extract sufficient resources to survive and to reproduce alone or in groups, competing and/or cooperating with others, both among our own and different species. Perhaps because of the scope of our actions, we seldom think, except in the most personal terms, about the impact of our behavior on our genetic lineage. Yet when one family lineage dies out, it is replaced by other competing lineages. This is why we can trace *Homo sapiens* all the way back to Mitochondrial Eve, for example. More colloquially, a colleague of mine tells an old story about a farmer who is thinking of buying a bull and asks the seller about the bull’s potency. “Well,” draws the seller, “he comes from a long line of fertile ancestors.”¹² The same is true for each of us.

I will apply to humans, at least for the purposes of generating hypotheses, the central paradigm in biology: What would it mean if humans, like other living organisms, have evolved to maximize their genetic contribution to future

generations through producing offspring and assisting nondescendant relatives such as nephews, nieces, and siblings? How will the particular strategies that accomplish such maximization differ in specific ways in different environments? And, just as for other mammals, how will these strategies typically differ between the sexes?

This is a complicated endeavor, at best. We change our own environments probably more often and more completely than any other organism. Further, history contains not only “selective” events, but events that are random with regard to fitness: when Mount Vesuvius erupted, the evolutionarily fittest Pompeian died as well as the least fit. Such histories complicate our problem: most of the time, we can expect the emergence of strategies that produce, compared to other strategies, the largest increase in genetic contribution—but sometimes sheer historical chance can alter what we see.¹³

Since we typically know so little about how much effect any particular genetic locus has on any specific behavior, behavioral ecologists assume that behaviors are the product of the *interaction* of genes and environment—not the result purely of genetics *or* environment. By using the phenotypic gambit, we assume that, when we look at behavior, we are seeing the result of gene-environment interactions over time and that the most common behaviors in an environment are working well compared to available alternatives. We ask when and how environmental conditions (including social conditions) change individuals’ genetic costs and benefits. If we understand how particular conditions are likely to affect behavior, and if we are cautious, we can predict the kinds of behavior we are likely to see.¹⁴

It is important to note that predictions are not absolute but statistical. We do not predict that genetically costly behaviors never arise, only that they will not become and remain common. Of course, there is a catch. Although we probably know more about the genes of *Homo sapiens* than of any other species except perhaps fruit flies, some yeasts, and some prokaryotes, we know the specific genetics of relatively few behaviors.¹⁵ Historical accident can present problems as well. The Pompeian tragedy probably changed human population genetics, at least locally. Thus we can get unexpected and interesting results from simple rules and historical accident.

Despite such complications, the phenotypic gambit is a good place to start—it works in many cases, helping us simplify and clarify what we see, as well as highlighting those behaviors that are more complicated than we had thought. When it doesn’t work, we have learned something valuable; when we do not find what we expect, we look for usually more complex alternative explanations. In animal behavior, this has proved to be an extremely powerful technique, as in the example of Heinrich’s ravens.

The rules may be simple, but rules never operate in a vacuum, and environments are varied and complex. Both physical and social/cultural environments are major determinants of what strategies will succeed. Humans are remarkably

complicated and flexible organisms, and human environments, with their elaboration of social and cultural rules, are multifaceted. There is little that tells us, in most cases, how important the various possible influences are or what the relative role of genes versus individual experience is. But if we ask about human behavior without assuming that humans are qualitatively different from other animals, perhaps we can get rid of the false dichotomy that has persisted between “biological” and “social” causes (both defined narrowly, with only proximate mechanisms considered as hypotheses).

Earlier “biological” hypotheses were typically concerned with, for example, whether sex differences could clearly be related to hormonal or brain lateralization differences. This is of interest but not related to (and not contradicting) questions about the evolution, or selective importance, of sex differences. “Biological determinism” has often been inferred from such observations that, for example, a behavior occurs in all cultures and/or a behavior occurs at a typical age. But to do this ignores the possible differences in the ecology of succeeding as a male or female mammal and simply makes assumptions based on analogy. It is surely misleading to construct a dichotomy between some sort of “biological/genetic determinism,” which is assumed to be fixed and immutable, and “social” causes of behavior, which are assumed to have no correlation with genotype. Most biologists now think that *all* behavior is likely to be the result of interactions between genes and environment and that experience is important for many species, not just humans.¹⁶

Both verbal and quantitative behavioral ecology differ from older approaches to behavior in two crucial regards: (1) currencies to be maximized are not simply economic or social but also genetic; and (2) following from this, an individual will treat others differently on the basis of what those others can do for that individual’s genetic representation, for example, treating kin and reciprocators better than others.¹⁷ We predict some widespread biases, and we can test for them. Thus, for example, “society” is not our primary concern as we dispense social and economic largesse;¹⁸ we typically leave our wealth to our children and nondescendant relatives unless we have none, or unless we have so much wealth that we can take care of our kin as well as endow foundations and chairs in universities (with, as a colleague noted, our family’s name attached).

With all these complexities, what then does behavioral ecology suggest about a view of “human nature”? It suggests that some traditional approaches have previously ignored an important currency: genes. It suggests that we do indeed look a lot like calculators but that we are not necessarily more conscious in calculation than other species, which may forage as optimally as if they carried Hewlett-Packard calculators in their cheek pouches, for example.¹⁹ It suggests that ecological constraints are important in setting limits to the strategies that will, and will not, “work,” and that human social complexity cannot be ignored.²⁰

Although genes are a currency, we seldom know the actual genetic influence on any particular trait, as I already noted. Using the approach I outline here, this

lack of information need not keep us from testing hypotheses. The questions we *are* able to answer, both in modeled systems like genetic algorithms and in empirical behavioral ecological studies of many species, including humans, are these: *In any particular environment what is the success of individual variants with different traits in reproducing?* and *How strong is the parent-offspring correlation in traits?*

Genes are more important in this view as a currency to be conserved and multiplied than as behavioral dictators, because external environment, development, and genes interact in a complex way. As the geneticist Theodosius Dobzhansky once put it: “Everything in the organism’s the result of the interactions of all genes, subject to the environment to which they are exposed. Inheritance is particulate, but development is unitary.”²¹ That is, although we conceptualize the effects of “a” gene as though it were separable, almost no gene acts alone; it is embedded along with other genes in a particular organism, which develops in a particular environment—and all this affects how the genetic influence plays out.

Many different particular internal mechanisms may be called upon to create complex behavioral responses. If we search too hard for the mechanism in each particular case, or if we ignore development and ecology, we may miss the forest as we stumble about in the trees. Consider this metaphor. The link between genes and bits of body or behavior is rather like the link between a cake recipe and the resulting cake. There is little one-to-one mapping. One cannot pick up this crumb and match it to that word or phrase in the recipe. Rather, the words of the recipe, like the genes in the chromosomes, together comprise a set of instructions for carrying out a process: development. In most cases, changing a word or phrase in the recipe will not change a particular crumb; more likely, it will subtly change the cake’s characteristics. Changing “baking powder” to “yeast” will change the cake considerably, but not in a particulate way. So will a recipe “mutation” to a sharply different oven temperature.²²

To extend the metaphor a little further, perhaps the reason we initially find this complexity confusing is that there are some well-known one-gene-one-trait correlations that seem particulate—like changing “walnuts” to “pecans”—and these have become quite famous. For example, the disease phenylketonuria arises from an individual getting two alleles for this disease at a single locus; this results in disturbed metabolism of phenylalanine (an important amino acid; the condition is diagnosed by a peculiar odor in the urine as phenylpyruvic acid is excreted) and leads to mental retardation.²³ So here is a case of a “one-word” (single locus) change that *is* particulate.

We are discovering other examples, and they make the front page of the news about once a month. But these dramatic single-gene effects can distract us from the ordinary, more subtle paths, and it is among these more subtle and complex interactive paths that I think we must look for the important links among environmental conditions, gene persistence, and observed behavior.

Hence, my focus is not on allelic specifics or precise models, but on more general problems that we're still learning to model precisely. As a classic text on behavioral genetics concluded, for the majority of behaviors studied so far, there is clear evidence of substantial genetic influence, though seldom any evidence of a really particulate single-gene-single-trait relationship.²⁴

Here, I focus on questions about the current utility, in selective terms, of different behaviors, with special interest in sex differences: What advantage, or disadvantage, accrues to an individual by virtue of having this trait in this environment?²⁵ This isn't always simple. The *process of optimization* (in each particular population, better strategies displace and replace inferior ones and the best *available* strategies prevail) is different from the *state of optimality* (the best imaginable fit between strategy and environmental conditions). Because selection acts only on existing variants, optimization is always local and often incomplete (these variants in this environment—some prevail, some disappear); as a result, we will see variety—perhaps a lot of rather similar, pretty-good varieties, not necessarily a settled, singular strategy.

Another difficulty in asking about utility or optimality is that one is asking about tradeoffs, and the “phenotypic correlation” can hide them. For example, suppose I hypothesize that, for an individual, what is spent on housing cannot be spent on transportation. So I would expect a negative relationship between housing and transportation expenses. But when I measure, I find a positive relationship. Does that mean that no trade-off exists? No, it probably means that I have compared quite incomparable individuals. If I compare not only graduate students, or hunter-gatherers in a particular society, but instead lump them together with professors and millionaires (who have enough money to own both a mansion and a Porsche), the range of variation obscures the trade-offs.²⁶

As we look at species, including our own, in a variety of environments—some quite new—we will find variety. We might find an excellent fit between trait and environment because of a long evolutionary history of unchanging selection. For example, the fact that Arctic fish can die of heat prostration at temperatures cold enough to freeze humans to death reflects for the fish a long selective history of constant cold. Or, we could see a trait that is currently advantageous, like running away from a fast-approaching truck. Since there were no trucks in the Pleistocene, the evolved rule was probably something like “run away from large, fast-approaching things,” and trucks, though relatively new, fit the same general category as dangerous fast predators of the Pleistocene. Because the process of optimization is complex and few traits can be easily isolated from developmental and historical constraints, we may rarely see a really fine-tuned “fit” between any single trait and environmental conditions.²⁷ Finally, humans seem to me to be at least as likely as any other species to show interpopulation differences not only as a result of natural selection and adaptation (perhaps sickle-cell anemia allele frequencies) but also because of historical—and cultural-historical—events (e.g., lactase distribution in humans; see chapter

10). There are very real difficulties, but I hope defining the problem as one of current utility may help avoid some of the less useful controversy.

This approach, I hope, creates natural linkages—to empirical fields of human behavior such as anthropology, psychology, and sociology on the one hand, and to ecology, genetics, behavioral genetics, and population theory on the other. Scholars in each of these (and other) fields have information and perspective on constraints and on how to consider human behavior. The “current utility” approach links us to what we know about other species as well.

We know something about the ecological and genetic components of behavior and about what behaviors become common under what circumstances, but our knowledge is still unconnected across disciplines; my work daily leads me to conversations with colleagues with whom I have more shared interests than shared knowledge. Now we need to reach across disciplines, and I hope experts in other fields will read this not as a postulated expert disquisition in their field but as an invitation to contribute what they know to solving the questions I raise.