Journal of Bioeconomics
https://doi.org/10.1007/s10818-023-09341-x

EDITORIAL

Ordinaries 13: apparent spite & apparent altruism

Terence C. Burnham[1] · **Jay Phelan**[2]

Abstract
Neoclassical economics assumes that people care only about themselves and, consequently, argues that people will not incur unrepaid costs to harm or help other people. In contrast, behavioral economics documents that people sometimes incur costs to hurt other people ('apparent spite') and in other situations incur costs to help others ('apparent altruism'). Biology argues that, in ancestral settings, such costly acts towards others were adaptive, and arose by natural selection because of benefits redounding to the selfish genes responsible for the behaviors. In evolutionarily novel settings such as cities, however, people will often incur costs that are not repaid.

Ordinary: "With no special or distinctive features; normal. Not interesting or exceptional; commonplace."

-Oxford English dictionary.

1 Self-interest is foundational to economics

"It is not from the benevolence of the butcher, the brewer, or the baker that we expect our dinner, but from their regard to their own interest." - Adam Smith's most famous quote.

Neoclassical economics generalizes the butcher, brewer, and baker quote. We act, in this standard view, to improve our own situation in life and do not care about others.

✉ Terence C. Burnham
burnham@chapman.edu

1 Chapman University, Orange, CA 92866, USA

2 Department of Life Sciences Core Education, UCLA, Los Angeles, CA 90095, USA

Published online: 25 November 2023

Economics, at its core, is concerned with understanding and predicting human behavior. As a consequence, it must have a model for human behavior. And the accuracy and value of economic findings depend on the degree to which its underlying model describes actual human behavior. As a model for human behavior, complete selfishness may appear to be a reasonable start.

Two types of human behavior, however, immediately challenge the neoclassical assumption of selfishness. In what we label 'apparent spite,' people incur costs to hurt others — seemingly gaining nothing for their efforts. Conversely, in 'apparent altruism,' people commonly incur costs to help others. (We explain our use of 'apparent' a bit later.)

As an example of apparent spite, consider the altercation between Darla Jackson and Zach Buob. On a California freeway, Jackson cut off Buob, who was driving his motorcycle. Buob then caught up to Jackson and kicked her car so hard that it left a dent and shoe print.

Jackson retaliated by chasing Buob, crossing all lanes of traffic and ramming into the back of his motorcycle, knocking him off, and running him over, killing him. Jackson, sentenced to prison, said, "I let pride get the better of me … it turned out terribly for everyone." (Effron, 2017).

Road rage is an example of spite; the payoff to each party is negative. We all experience spiteful interactions, albeit usually not leading to death. In 2019, the FBI reported that 600 people were beaten to death in the US with 'hands, fists, or feet.' In the same year, 397 people were clubbed to death with hammers or other objects, 1,476 were stabbed to death, and more than 10,000 were shot to death by others (FBI, 2019).

A neoclassical economist would never fear a physical confrontation with a stranger in situations where the other person can gain nothing. Such conflict is spite — bad for both parties — and does not exist in the neoclassical model of human nature. A maximizing-utility person would never engage in spiteful activity; to do so would be irrational.

In a further surprise to neoclassical economists, the world appears to be full of altruistic actions. For example, there are more than 20,000 living kidney donations per year in the world (Horvat et al., 2009). In a living donation, the donor gives one of their two kidneys to another person. Most of these are between family members, but some are between complete strangers (Sharif, 2013).

Apparent spite and apparent altruism are the subject of this article. Within economics, the assumption of self-interest plays a central role in understanding and predicting human behavior. Neoclassical economics assumes that people derive pleasure from their possessions and their own leisure — a fancy car and a drink on a beach, perhaps. People do not, in the neoclassical view, derive pleasure from running over strangers on the highway or undergoing surgery to donate body parts.

In sharp contrast to the neoclassical perspective, behavioral economics argues that people have 'other-regarding preferences,' meaning that humans can and do obtain pleasure and pain from the outcomes of other people (Cooper & Kagel, 2016). The battle over self-regarding or other-regarding preferences is a fundamental disagreement within economics about human nature.

The schism between neoclassical and behavioral economics on interpersonal preferences mirrors the disagreements about attitudes toward time (Ordinaries 5, Burnham & Phelan, 2021a), toward goods (Ordinaries 6, Burnham & Phelan, 2021b), and for risk (Ordinaries 10, Burnham & Phelan, 2022c).

For each axiom of economics, there is a dispute, always hinging on some belief about human nature. The axioms of neoclassical economics are assumptions that are grounded in nothing, and are not derived from some larger, encompassing theory. Behavioral economics is similarly without any foundational theory; simply cataloging human behavior that deviates from actions predicted by neoclassical economics.

The Ordinaries approach uses natural science methods for elucidating truths about human nature to improve economics' understanding of human behavior. This article explores attitudes toward other people, within the mission of this series (Burnham & Phelan, 2019, 2020a, b, c, 2021a, b, c, 2022a, b, c, 2023a, b):

> The Ordinaries column will interpret economic behavior from the perspective of evolutionary biology. From this view of life, the anomalies of behavioral economics will disappear into a coherent biological framework that incorporates elements of neoclassical maximization.

2 Economic views of apparent spite & apparent altruism, without the help of biology

2.1 Neoclassical economics assumes selfishness

Self-interest is at the core of economics. People are assumed to maximize utility. In abstract economic theory, that utility could be derived from other people. In practice, however, neoclassical economic models assume utility is derived from individual outcomes.

In other words, self-interest differs, in principle, from selfishness. A self-interested person could become happy by giving all their money to a stranger. A selfish person, in contrast, derives satisfaction directly from their own life. Self-interest in economic theory is selfishness in economic practice.

Selfishness is manifest in the individual's approach to maximizing utility. The neoclassical assumption is that each person seeks to work as little as possible, and to acquire as much material possession as possible. Mathematically, the neoclassical assumption is that individuals maximize utility — derived by individual leisure and consumption (TVs, cars, house, vacations, steaks, etc.), and with each individual being constrained by the amount of money they have available.

2.2 The selfishness assumption matters

Does it matter that self-interest in neoclassical economics is selfishness? Yes. An example that we have described previously is David Ricardo's concept of comparative advantage.

Apocryphally, an economist and a physicist were arguing at Harvard's famous Society of Fellows. Mocking economics, the physicist challenged the economist to "tell me one finding of economics that is true, important, and non-obvious." Here is the substance of the economist's retort.

David Ricardo, 18th and 19th-century economist, changed the world with the theory of comparative advantage. At the time, mercantilism was the central idea of economic and political practice.

A mercantilist tries to accumulate as much wealth as possible. An apparent and obvious approach to having as much money as possible is to sell goods to others but buy as little as possible from them. England, for example, under a mercantilist system, would sell products to Spain in return for gold, but aim to use none of that gold to buy products from Spain.

Ricardo developed the theory of comparative advantage which demonstrates that England can become richer by buying products from Spain, even if England were better at producing every type of product.

Before the Tiger Woods scandals, the most famous economic textbook introduced comparative advantage by asking if Tiger Woods should mow his own lawn. Tiger — with tremendous fine-motor-control — could likely produce a fantastic edge and consistent grass height. It seems reasonable to suggest that Tiger could do an amazing job cutting grass. But he shouldn't. Why? Because Tiger Woods can use his time more productively elsewhere.

Tiger Woods may have an 'absolute' advantage in lawn cutting, meaning that his mowing can produce a better lawn than could be produced by the person that he hires. The lawn mowing service, however, has a 'comparative' advantage, however, in cutting the grass because it allows Tiger to perform other, more valuable, activities.

David Ricardo is right. Comparative advantage is correct and non-obvious. It is so non-obvious, in fact, that many countries made themselves poorer by following the proscriptions of the intuitive, but incorrect, mercantilist theory. Comparative advantage also satisfies the third attribute of importance; entire economies were improved by Ricardo's theory.

What does comparative advantage have to do with self-interest and selfishness? Comparative advantage and free trade can make both countries (or every country, in multilateral trade) richer. If the people in those societies care only about material wealth, then acting according to comparative advantage will make people happier.

If, however, people care about others — and, in particular, if they care about relative wealth — then trade may not cause people to feel better off in their own self-evaluation. Would you want to enter a deal with your rival where you made \$1 and your rival made \$1 billion? If not, you are not behaving as assumed by neoclassical economics.

The relevant point is that all of economics, even the most successful and brilliant theorems, are dependent on assumptions about human nature. Comparative advantage argues that both trading parties can be made better off by trade. However, and generally unstated, is the assumption that people's happiness comes from their own consumption, and is not influenced at all by the outcomes for other people.

David Ricardo is correct that comparative advantage allows both parties to become richer through trade. However, if neoclassical economics is wrong about the

Table 1 A taxonomy of behavior (based on Hamilton, 1964a, b)

		Impact on Recipient	
		positive	negative
Impact on the Actor	positive	Cooperation	Selfishness
	negative	Altruism	Spite

Table 2 Economics of apparent spite and apparent altruism without the natural sciences

Phenomenon	Individuals are inconsistent in their attitudes toward other people. People are sometimes spiteful and at other times altruistic.
Neoclassical economics	Individuals care about themselves and derive no pleasure or pain from the lives of others, not even their own children.
Behavioral economics	People are sometimes spiteful in incurring costs to hurt others and sometimes altruistic in incurring costs to help others.

irrelevance of interpersonal evaluations to an individual's preferences, trade may not make both parties happier.

2.3 A framework for classifying behavior

Let's recap. Neoclassical economics assumes that people are selfish, caring only about their own individual situation. This selfishness assumption plays a central role in economic theory. If, on the other hand, people are not selfish, but rather behave in ways that are apparently spiteful or apparently altruistic, then economic theory needs to be revamped.

To explore this possibility, let us define spite and altruism carefully. The important biologist W.D. Hamilton laid out a framework for categorizing behavior based on the biological payoff (in terms of evolutionary fitness) to the 'actor' and to one or more 'recipients' (see Table 1). Note that this is exactly how economists approach human behavior, but with one critical difference: a consideration of the *biological* payoff.

In Hamilton's 2×2 matrix, there are four types of behavior, categorized by the impact of the behavior on the actor and on one or more recipients.

- **Selfishness** is good for the actor and bad for the recipient.
- **Cooperation** is good for the actor and good for the recipient.
- **Altruism** is bad for the actor and good for the recipient.
- **Spite** is bad for the actor and bad for the recipient.

Neoclassical economics assumes that people will only behave in ways that lead to gain for themselves. In Hamilton's framework, neoclassical economics assumes that we will observe selfishness and cooperation, but never spite or altruism.

2.4 Behavioral economics focuses on laboratory studies, not the real world

Behavioral economics argues that neoclassical economics is wrong; people are, in fact, sometimes spiteful and sometimes altruistic (See Table 2).

Most people who are not economists would immediately agree with the behavioral economic view. In the introduction, we discuss Darla Jackson killing Zach Buob in a road rage dispute. In a recent survey, 78% of drivers admit to tailgating, yelling, honking, or committing other aggressive driving behaviors (Octo, 2022).

For those of us who drive, conflict with strangers is ubiquitous. Additionally, in other areas of our life, we commonly see apparently altruistic acts, ranging from minor acts of kindness to life-saving organ donations. We noted 20,000 living kidney donations per year.

Giving up a kidney is an extreme act, but another type of tissue-donation procedure may be even more extreme. A large number of people donate part of their liver. A study of 1,508 such live liver donations documents the impact on the donor. Under the best of circumstances, the donor stays in the hospital for weeks. Furthermore, significant numbers of donors suffer from severe side effects including thrombosis, 'bile leakage,' and even death (Lo, 2003).

In order to document spite and altruism, do behavioral economists document street fights and bile leakage caused by liver donations? No. These actions are, intentionally, never mentioned. Rather, the focus of behavioral economics is on (seemingly trivial) decisions made in economic experiments under laboratory conditions. For example, in an economic game, Phoebe paid five dollars to take thirty-five dollars from Ted, thereby demonstrating spite.

To understand why behavioral economics focuses on seemingly irrelevant behavior, let us return to Ordinaries 1 (Burnham & Phelan, 2019). In the big picture, neoclassical economics assumes good (actually perfect) decision-making, while behavioral economics argues that people often make bad decisions.

In Ordinaries 1, we suggest four types of behaviors that would seem to support the behavioral economic view that people are not maximizing anything. (1) Opiate use. (2) Insufficient saving for retirement. (3) Early death and disease through diet and lifestyle decisions, and (4) Suicide.

Behavioral economics does not discuss drug use, lack of savings, sedentary lifestyles or suicide, but rather focuses on apparently trivial, often small-stakes, laboratory behavior. In the first Anomalies article, Richard Thaler focuses on (and is shocked by) people's illogical behavior in an abstract-logic-testing, card-flipping task (Thaler, 1987).

Why does behavioral economics ignore suicide, murder, kidney donation, and death by opiates, and instead focus on mismanaging pennies in laboratories? The answer is that behavioral economics is a within-the-discipline critique. The neoclassical economics perspective is actually consistent with individuals in some situations choosing murder, suicide, drug addiction, and all other seemingly-destructive behaviors.

When it comes to spite and altruism, real-world behaviors on the road or in the kidney transplant center do not violate neoclassical economics. This is because in these cases, the target behaviors may generate future repayment through reputation enhancement.

The kidney donor may be lauded as an altruist and, as such, accrue benefits, jobs, spouses, gifts, etc., that more than compensate for the risk and the negative health consequences of living with just one kidney. Similarly, showing toughness on the roads may build a reputation for fierceness that gets rewarded in other settings.

Because actions in the real world have reputational consequences, truly costly actions must involve incurring those costs in very particular environments; settings where repayment is not possible. That is why behavioral economists resort to looking for irrational behaviors in the context of playing laboratory games for small amounts of money with strangers.

2.5 Laboratory experiments documenting spite and altruism

Behavioral economics documents spite and altruism, primarily in laboratory settings where behavior is non-repeating, final, and anonymous.

Would you accept $1 from a stranger? What if the stranger had been given $100 and also given the right to make you a take-it-or-leave-it offer? So the $1 actually comes in the form of an ultimatum:

Accept my $1 out of $100, and I take $99. Or get nothing and I also get nothing.

Rejecting this sort of ultimatum is spite as defined above in WD Hamilton's taxonomy. The rejection has a true cost for the actor. By rejecting the offer, they lose out on $1. But the rejection also inflicts a larger cost on the other person, who will not get $99.

This much-replicated 'ultimatum game' has been analyzed by economists. According to the analyses — using standard assumptions of rationality — the conclusion is that people will not be spiteful. Ever. Rather, they will accept any amount of money greater than zero, regardless of any impact their acceptance has on the person making the offer.

The first experimental ultimatum game was published in 1982 (Güth et al., 1982). It was conducted in Germany for about $10 US dollars. The participants never knew who they were interacting with, and the outcome was final. After the ultimatum, the people were paid (if the proposed split of money was accepted), and left the laboratory one at a time, so they wouldn't see each other.

To neoclassical economists, this game should appear completely uninteresting (and completely predictable). Those deciding how to split the money will propose the split that gives them the most money allowed. And those deciding whether to accept or reject the offer will take the money, regardless of how much or how little it is and how much the proposer will get to keep for themself.

What actually happened in this first ultimatum game? One behavior commonly occurred that was — from the neoclassical economics perspective — irrational and surprising. A significant number of people were spiteful. They rejected offers that were a small percentage of the total.

Anyone who has ever felt rage toward a rude driver not following the rules of merging onto a highway would be completely unsurprised by the fact that people can be spiteful.

Economists, however, were shocked! The original ultimatum game paper has been cited by more than 6,000 academic studies. The overall field of 'other-regarding preferences' may have more than 100,000 published academic papers. Given that each paper can take a year or longer, this is a tremendous amount of effort. (We'll discuss below why biologists are not shocked — and, in fact, would have been stunned by any other results).

People are spiteful, too, in many other behavioral economics studies in addition to the ultimatum game. That is, people will choose to incur costs that can never be repaid, in order to inflict costs on others.

Not only are people spiteful in economic games, with small changes to the games they can — reliably — be made to behave altruistically. An altruist incurs a cost to give extra money to one or more other recipients.

The simplest 'game' showing altruism is called the 'dictator game.' In the dictator game one person is given some amount of money and told they can keep it all or give some to an unknown stranger sitting in another room who they will never see. In the dictator game, experimental subjects routinely give money to other people.

And so, to summarize: behavioral economics has documented that, like road-ragers and kidney donors, people can sometimes be spiteful and sometimes be altruistic.

2.6 The key findings of behavioral economics are not new

Has behavioral economics gone beyond documentation of the phenomenon of altruism and spite to develop a theory of human behavior, incorporating this sort of motivation? No.

"Happiness springs from doing good and helping others." This quote is frequently attributed to Plato. We can find no evidence for this exact quote, but it is consistent with Plato's view that happiness is attained by living a virtuous life that requires treating others well.

Overall, our critique of behavioral economics is that the field frequently contributes nothing to our understanding of human nature beyond what has been known since the dawn of humanity. Consider this passage by Plato:

> The wild beast within us, gorged with meat or drink, starts up and having shaken off sleep, goes forth to satisfy his desires; and there is no conceivable folly or crime — not excepting incest or any other unnatural union, or parricide, or the eating of forbidden food — which at such a time, when he has parted company with all shame and sense, a man may not be ready to commit.
>
> A man must take with him into the world below an adamantine faith in truth and right, that there too he may be undazzled by the desire of wealth or the other allurements of evil, lest, coming upon tyrannies and similar villainies, he do irremediable wrongs to others and suffer yet worse himself. (Plato, pg. clv, in Jowett, 1888)

With respect to spite and altruism, Plato notes that without self-control, parts of human nature will lead us to treat others poorly, and this will decrease our own happiness. Furthermore, he recognizes the internal battle for self-control, an aspect of human nature assumed not to exist by neoclassical economics.

Finally, a virtuous life requires constraining our beast nature and denying our desire to gorge ourselves. However, gorging ourselves is assumed by neoclassical economics to be the goal of life; we maximize utility, in the neoclassical view, precisely by feeding the beast. Plato recommends that people be ‘undazzled by the desire for wealth.’ The goal of life, according to neoclassical economics, is to gorge oneself on wealth.

Thus, Plato captures key elements of human nature that are inconsistent with neoclassical economics. One could argue that Plato was the first behavioral economist. However, that would be wrong. There were millions of behavioral economists before Plato — they are called people. You don’t need to be Plato to understand human nature better than the neoclassical economic model of human nature.

All humans that have lived for more than a few years — including those who lived before the invention of writing — learn that people are sometimes apparently spiteful and sometimes apparently altruistic. Consider that ‘schadenfreude’ — getting joy from other people’s failures or pain — is seen in children as early as 24 months of age (Shamay-Tsoory et al., 2014).

So behavioral economics has documented the fact that, within the economic paradigm, people sometimes incur costs to help others, and at other times incur costs to hurt other people. As virtually all people have known since the beginning of humanity, the neoclassical assumption of selfishness is not correct. Now what? Table 2 summarizes economic views of apparent spite and apparent altruism without the insights of the natural sciences.

2.7 Economics is currently stuck in Stage 2 of Kuhn’s framework

The economic debate regarding interpersonal preferences fits well into Thomas Kuhn’s paradigm for the structure of scientific revolutions (Kuhn, 1962, 1970). Stage 1 is the existence of a dominant paradigm. Stage 2 is the accumulation of divergences, labeled ‘anomalies,’ that are inconsistent with the dominant paradigm. Stage 3 is the introduction of a new framework, which incorporates the anomalies into parts of the prior model.

Stage 1 in the Kuhnian framework for apparent spite and apparent altruism is the selfish version of the neoclassical model. In this Stage 1 model, each individual person works as little as possible and consumes as many products, services, and experiences as possible. The individual derives nothing from the outcomes of other people — positive or negative — not even their own children. The goal is to maximize utility by being maximally selfish.

It is somewhat stunning that the neoclassical model was relatively accepted — at least within economics — up until the first ultimatum game publication in 1982. As noted, Plato wrote about concern for others, as did Adam Smith in the Theory of Moral Sentiments, “To feel much for others and little for ourselves, that to restrain our selfishness, and to indulge our benevolent affections, constitutes the perfection of human nature” (Smith, 1759, Chapter V).

Stage 2 in the Kuhnian framework is the behavioral economic work documenting that people care about what happens to other people, even people who are not genetic relatives.

Here is a summary of the behavioral economic view, “People prefer more money to less, like to be treated fairly, and like to treat others fairly. To the extent that these objectives are contradictory, subjects make trade-offs. Behavior also appears to depend greatly on context and other subtle features of the environment" (Thaler, 1988, p. 205).

Stage 3 in the Kuhnian framework is a realigned economics, grounded in biology, and which moves beyond the debate about whether people are selfish or not. Human behavior, including economic behavior, is the product of evolution by natural selection and generated by physiological mechanisms that are flexible and sensitive to the environment.

Depending on the environment, people's behavior may appear to be spiteful or appear to be altruistic.

3 Biological insights into apparent spite and apparent altruism

3.1 Natural selection favors genes that enhance the relative reproductive output of the individual possessing them

The great value of Darwin's theory of evolution by natural selection (Darwin, 1859) is that it provided a framework for understanding the diversity of life forms that we see on earth. Why do giraffes have long necks? Why do peacocks have giant, elaborate tail feathers? Why do sharks have rows of razor sharp teeth? Why are some insects almost-perfect mimics of the leaves on which they graze?

Darwin's idea was straightforward, and depended only on whether three simple conditions were satisfied.

1. *Is there variation for a trait within a population of organisms?*
2. *Is that trait heritable?*
   (Put another way: Do offspring resemble their parents for the trait more than they resemble unrelated individuals?)
3. *Is there differential reproductive success based on the trait?*
   (Put another way: Do individuals with some versions of the trait leave more offspring than individuals possessing other versions of the trait?)

When these three conditions are satisfied, evolution by natural selection occurs. And, as a consequence, populations of organisms can become beautifully adapted to their environment. This occurs in all species, regardless of whether the organisms are insects or microbes or fruiting plants or humans.

It is easiest to see the outcomes of evolution in the form and function of organisms' physical features. But natural selection shapes any trait that satisfies those three conditions. Even behaviors: the choices an animal makes when choosing what to eat, the ways an animal courts a potential mate, the strategies by which an organism evades predators (Phelan, 2021).

In stark contrast to the prevailing worldview at the time, Darwin's idea implied that organisms were not created de novo in their present forms. Populations do not remain perpetually unchanged in the traits possessed by their individuals. The great value to this understanding of life is that it enables us to observe populations and elucidate the reasons why some version of a trait — any trait — is present.

The version of a trait we see must have resulted, over evolutionary time, from those individuals possessing it leaving more offspring than were left by individuals possessing alternative versions of the trait.

Darwin appreciated this fact from the very beginning. In *The Origin of Species* he even revealed how this was cause for concern for him: "I will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory. I allude to the … sterile females in insect-communities … they cannot propagate their kind."

Darwin understood that, according to his theory, evolution by natural selection could not lead to a trait which caused the organisms possessing it to ***not*** produce more offspring than those with an alternative version of the trait.

Because his theory explained the vast diversity of traits he observed and documented among populations around the world, Darwin did not abandon it based on the seeming problem presented by sterile honeybee workers. Perhaps, with additional knowledge, their existence might be reconciled. And indeed, one hundred years later, biologists came to understand how natural selection could even favor the production of sterile individuals within a population (Hamilton, 1964b). (More on this specific case later.)

Other biologists were similarly perplexed by some behaviors they observed. Given their understanding that natural selection produces traits that enhance the relative reproductive success of the individuals possessing them, how could it be possible that we observe individuals behaving in ways that seem altruistic?

* An Australian social spider allows her many offspring to pinch her body and suck the fluids out of her — ultimately causing her to die, unable to produce additional offspring (Seibt & Wickler, 1987; Evans et al., 1995).

* A vampire bat just returning from foraging regurgitates calorically-rich blood into the mouth of another, unrelated, individual, that is starving and begging for food (Wilkinson, 1984).

* A ground squirrel detects an approaching predator and, rather than running for cover, screams loudly. This alerts nearby individuals to the danger and enables them to escape death, while putting the screaming squirrel at a significantly increased risk of death (Sherman, 1977, 1985).

Put another way: **Why do we see so many acts of apparent kindness in the world?**

As we explain below, apparently altruistic behaviors are exactly that: "apparently" altruistic. Inspection from an evolutionary perspective reveals that such behaviors are not *actually* altruistic. They only appear so in isolation from their larger context.

3.2 Natural selection can produce apparently altruistic behaviors

We use the terms ‘apparent spite’ and ‘apparent altruism’ because these actions are not actually spiteful or altruistic. Rather, they increase the prevalence of the underlying genes.

The puzzle of apparent spite and apparent altruism has been solved within biology. Costly voluntary acts are produced by genetically-encoded physiologic mechanisms that evolved because the behaviors — which *appear* to be altruistic or spiteful — actually redound to the benefit of the genes.

In this section, we describe two pathways by which evolution by natural selection can produce apparently spiteful behaviors as well as apparently altruistic behaviors. In each case, we’ll see that apparent spite and apparent altruism are actually – evolutionary – genetic selfishness. For those interested in a longer account than we have space for in this article, we suggest West et al. (2007a).

There are two pathways by which apparently costly behavior can arise:

1. **Apparent spite (and altruism) that is repaid.** For example, the version of a gene you possess causes you to help some other individual, who will return the favor in the future, thereby helping you (and the version of the gene causing the apparent kindness). In a sense, the gene buffers itself from an uncertain future by storing goodwill in others. Alternatively, the costly act may be repaid in some other manner by altering the behavior of other people.
2. **Apparent spite (and altruism) that directly benefits the genes producing such behaviors.** An action may be bad for the organism but good for alleles possessed by that organism. For example, an allele in you causes you to act in such a way that you increase the reproductive success of other individuals carrying that allele, such as siblings or cousins, who inherited it from the same ancestor as you.

In both cases, a gene’s eye view of the world illuminates how apparent spite and apparent altruism can increase a gene’s payoffs, relative to alternative versions of the gene.

3.3 Apparent spite (and altruism) that is repaid

3.3.1 Reciprocal altruism

The first pathway to apparent spite and apparent altruism involves costly behaviors that produce benefits in the future. Seen in isolation, the actions may seem costly with no apparent payback, but they are part of a longer-term strategy.

The term ‘reciprocal altruism’ is used to describe repayment by the same person who benefits from a favor. The seminal paper — cited more than 16,000 times — is entitled “The evolution of reciprocal altruism” and was published by Robert Trivers in 1971. For his work on social behavior, Trivers won the Crafoord prize, which is harder to win than the Nobel prize.

People have friends. They do favors for their friends. They get mad if they are slighted. They get into arguments with friends. Surely, you might think, this was known to all humans.

How does one win a prestigious prize for identifying the existence of reciprocal altruism? Part of the answer is that the role of evolution and genes in human behavior was entirely novel to biologists in the middle of the twentieth century (much as it is to economists today).

We have always admired the original reciprocal altruism paper because it provides an ultimate explanation, in the Tinbergen framework, for the gamut of human emotions. In the paper's abstract, Trivers concisely describes the idea and its far-reaching implications: "friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, and some forms of dishonesty and hypocrisy can be explained as important adaptations to regulate the altruistic system" (Trivers, 1971, p35).

Conditions that favor reciprocal altruism include repeated interactions between individuals, a high benefit to the recipient relative to the cost to the actor, and an ability to keep tabs on individuals and to punish non-reciprocators.

Reciprocal altruism has significant adaptive value for individuals, allowing them to flourish much more than they can on their own (see, for example, Lewis et al., 2007; Wilkinson, 1984, 1988). But it also is fraught with risk; we are very vulnerable (from an evolutionary perspective) when we help another person. A cheater can take the favor and run, thereby causing the market share of their "cheater genes" to increase, and the market share of the "reciprocal altruism genes" to decrease.

For these reasons, reciprocal altruism helps illuminate why such strong emotions regulate friendships. "Why do I get so mad that I wasn't invited to a birthday party?" The answer is that we are built to carefully monitor relationships and be ready with what Trivers calls "moralistic aggression" to punish transgressions. For example, when a group of friends dine out together, some people never seem to pay their full share. Do you remember who those cheapskates are? (Yes. We all do.)

Reciprocal altruism explains some apparently spiteful and apparently altruistic actions as part of a mutually-beneficial relationship between two parties. Consider the vampire bats mentioned above. The bats suck blood for their nourishment, but on any given night about 10% of adults and 33% of juveniles fail to find a meal. Owing to their small body size, a bat will starve to death if it fails to obtain food for three nights in a row.

Back at their roost, hungry bats beg for blood from successful foragers, who will, on some occasions, regurgitate a blood meal into the hungry bat's mouth. This comes at a cost to the bat giving up the blood meal, but can save the life of the hungry bat. From numerous long-term research studies, we know that a bat is significantly more likely to give food to bats that have previously helped it and more likely to shun individuals that have not helped them (Wilkinson, 1984; Carter & Wilkinson, 2013, 2015; Carter et al., 2017).

3.3.2 Indirect reciprocity

In reciprocal altruism, the costly act is repaid by the recipient. Trivers, in the same 1971 paper, and then further in his book *Social Evolution* (Trivers, 1985), also discussed the possibility of repayment by someone other than the recipient. In Trivers' words, "An individual does not necessarily receive reciprocal benefit from the individual aided but may receive the return from third parties." (Trivers, 1985, p. 389).

'Indirect reciprocity' is the now-accepted term for Trivers' notion of repayment by a third party (coined in Alexander, 1987). In indirect reciprocity, there is value in maintaining a good reputation to garner benefits from others. To cite one modest example, restaurants with higher social media ratings are less likely to go bankrupt (Lu et al., 2018).

Apparent spite, in the form of costly conflict, is not actually spite if the aggressor gets repaid. A review of the literature concludes, "individuals often punish other group members that infringe their interests, and punishment can cause subordinates to desist from behavior likely to reduce the fitness of dominant animals" (Clutton-Brock & Parker, 1995, p. 209).

Consider the behavior of female mountain goats, *Oreamnos americanus*. These goats fight each other for status: "Compared with other female ungulates, mountain goat females interacted aggressively much more frequently, and their dominance ranks were less stable in time and less age-related" (Fournier & Festa-Bianchet, 1995). Big females with large horns are more likely to win such dominance battles, but as noted, rank is unstable, and fights are sometimes won by the small females.

If a behavioral economist observed a female goat fight in a laboratory between animals from different groups that would never see each other again, they might label the behavior as spite. The fight is bad for both animals, and because they do not know each other and will never interact with each other again (the standard setting for behavioral economic studies), there is no way that the costs of fighting can be recouped in the future.

In the wild, however, fights between female mountain goats are part of a long-term, adaptive strategy where dominant animals resist subordinates. Obtaining higher rank pays off, as "Social rank appears to be an important determinant of reproductive success for female mountain goats, especially among young females" (Côté & Festa-Bianchet, 2001, p. 173). Although in studies like these, among wild animals, the results are correlations not definitive proof of causation.

Similarly, costly fights to establish male chimpanzee rank translate into the evolutionary benefit of higher reproduction. In one long-term study of the relationship between status and reproductive success among wild chimpanzees, the single highest-ranking male sired 50% of all the offspring that were DNA-sequenced to establish paternity (Boesch et al., 2006).

The same correlation between male rank and reproduction is found in a wide variety of species. For example, a meta-analysis of 32 studies concludes, "a reliable positive relationship between male dominance rank and mating success amongst animals of the same age class is seen" (Cowlishaw & Dunbar, 1991, p. 1045).

In a social setting where people have reputations, and others alter their behavior based on those reputations, it can pay to boost one's reputation through apparently spiteful or apparently altruistic actions. Recall the study reporting positive reputation enhancement for giving money to homeless people (Iredale et al., 2020). A laboratory study investigated the relationship between contributions to help others and within-group status, finding that "the most altruistic members gained the highest status" (Hardy & van Vugt, 2006, p. 1402).

3.3.3 Costly signaling

Costly or honest signaling is another type of behavior favored by natural selection, in which costly, voluntary actions have no immediate repayment (Spence, 1978; Zahavi, 1975). In honest signaling, an organism undergoes some cost, which informs the world about its quality. Because of paying the price for generating the signal, the organism receives extra benefits that exceed the cost.

Consider the bright, large tail of a peacock. The tail is a huge hindrance to navigation and a giant sign that says "eat me" to predators. Why does the peacock have such a large and colorful and costly tail? The signaling hypothesis is that peacocks that have large tails and live to mating age must have strong genes for other attributes. Therefore, females ('peahens') can use the size of the peacock tail as a signal of male genetic quality.

Is the male peacock tail a costly signal of quality? Yes, according to several studies. In these studies, peahens were randomly assigned to mate with males with long or short tails. The offspring of males with long tails were larger and more likely to survive (Petrie & Williams, 1993; Petrie, 1994). So, males with longer tails produce better offspring; peahens, when free to choose, prefer males with longer tails (Petrie et al., 1991, but see also conflicting data in Takahashi et al., 2008).

Physical signaling — including the peacock's tail — may be the most well-known example of incurring a cost to accrue later benefits. Here, however, we are more interested in costly behaviors.

It is hypothesized that acts of apparent altruism signal underlying quality in people (Barclay, 2006; Iredale & van Vugt, 2012). Consistent with this hypothesis, researchers have documented that apparent altruism is significantly correlated with mating success (Arnocky et al., 2017) and other reputational benefits (Roberts et al., 2021). The person exhibits apparent altruism not because of intrinsic joy from helping others, but because such actions can be a signal of quality that induces others to bestow benefits on the apparent altruist.

Some of the clearest evidence for the long-term evolutionary benefit of costly signaling comes in non-human animal behavior. Consider the behavior of a species of lemur, known as Verreaux's sifaka (*Propithecus verreauxi*). Male sifakas can engage in behaviors that produce a stain labeled by some as a 'chest badge.' The stain is produced on an otherwise clean chest by vigorous chest rubbing and scent marking (Dall'Olio et al., 2012).

Obtaining chest badges for Verreaux's sifakas is voluntary and costly. The cost is both the direct energetic cost of creating the stain, as well as the increased chance of physical fighting. When two male sifakas meet, if one of the two is clean-chested, then that male submits, making subordinate grunts. The cost of the interaction is lower than when two males sporting chest badges meet (Lewis & van Schaik, 2007).

Why incur the direct and indirect cost of producing chest badge and subsequent fighting with others having chest badges? Considered in isolation, such behavior fits the definition of apparent spite: costly to the individual and costly to others.

The chest badge is hypothesized to be a costly signal of male quality (Dall'Olio et al., 2012). Being able to incur the costs of the badge signals to potential mates that the badged male is genetically better. And in fact, males with chest badges do mate significantly more frequently.

Chest-marked males mated once every two hours vs. less than once per five hours for clean-chested males (Dall'Olio et al., 2012). Clean-chested males employed a grooming strategy to gain access to mating, but badged males were always able to displace clean-chested males, even if mating had already begun.

A final interesting set of data is consistent with the costly signaling hypothesis. Chest-marking is not correlated with body size but is correlated with testosterone levels (Lewis & van Schaik, 2007; Kraus et al., 1999).

To summarize: Viewed in isolation, costly signaling appears to be an irrational act of spite or altruism. With an evolutionary perspective, we can understand that it is a genetically selfish behavior, influencing reputation and, in turn, the behavior of others. The costly act is, ultimately, rewarded with increased relative reproductive success.

3.4 Apparent spite and apparent altruism that directly benefits the genes producing such behaviors

In the second evolutionary path to apparent spite and apparent altruism, the organism is never repaid, but the genes responsible for the behaviors still increase in relative abundance within the population. We discuss the three most important ways that the frequency of such genes can increase, even if they carry a cost to the organisms carrying them.

"Bob's your uncle" is a British phrase based on the common appearance of nepotism — helping one's nephews and other genetic relatives. The Earl of Balfour was a British statesman whose career was far more prominent than his apparent qualifications. In 1874, Balfour was appointed Chief Secretary for Ireland, a position for which he did not appear to be qualified. The popular explanation was, "Bob's your uncle." This was in reference to Balfour's uncle, Robert ("Bob") Cascoyne-Cecil, who happened to be the prime minister of the UK.

With Bob as his uncle, Lord Balfour rapidly ascended the ranks in the government, eventually succeeding his uncle as prime minister in 1902. Nepotism, derived from the Latin *nepōs*, meaning nephew, is the practice of helping one's relatives other than direct descendants. If you help your child, that is parenting, not nepotism. If you help your niece or your cousin, that is nepotism. Nepotism in human behavior presumably predates writing; both Aristotle and Plato harshly condemned nepotism.

Given the long history of nepotism in human affairs, it is perhaps surprising that biological explanations for nepotism arose only in the 20th century. The remaining biological explanations for apparent altruism are all based on the same idea. Evolution by natural selection leads to an increase in the frequency of those versions of genes that have higher replication rates than alternative versions of the genes. In other words, if a gene causes more copies of itself to be present in subsequent generations, that gene's 'market share' increases.

How does a gene win the evolutionary competition? The most direct route is to improve the reproductive output of the organism. For example, a gene that provides better echolocation in a bat improves the animal's survival and reproduction.

However, a different route is for a gene to induce behavior in which an individual sacrifices its own outcome in order to increase the outcome of other individuals carrying the gene — thereby increasing that gene's market share relative to other existing variants of the gene. This idea of "bad for the organism, good for the gene" is the basis of kin selection, rational spite, and group selection.

3.4.1 Kin selection

W.D. Hamilton first recognized, described, and mathematically derived the concept of "kin selection," explaining that apparently-altruistic actions directed toward genetic relatives reflected genetic selfishness (Hamilton, 1964a, b).

Kin selection is often expressed using a simple equation referred to as "Hamilton's rule." It expresses that costly actions that help others are favored by natural selection as long as the benefit to the recipient exceeds the cost to the actor, after accounting for the closeness of the genetic relationship.

In the case of nepotism, an uncle shares one-quarter of his genes with a nephew — by virtue of the uncle and nephew sharing a recent common ancestor. Hamilton's rule states that evolution favors uncles who are willing to incur a cost of 1 to create a benefit of at least 4 for a nephew.

The famous biologist J.B.S. Haldane allegedly quipped (Maynard Smith, 1975), that he was prepared to lay down his life for eight cousins or two brothers (or, unstated, four nephews). Cousins share, on average, one-eighth of each other's genes, due to their recent common ancestors. Hence the eight-to-one ratio in Haldane's comment.

No one is surprised that evolution favors parents who sacrifice for their children. The children are the most direct genetic route to evolutionary success. Nephews and cousins provide a similar, if somewhat diluted and indirect, route to genetic success.

Mathematically, Hamilton's rule states that natural selection will increase the frequency of behaviors for which $B*r>C$, where B is the fitness gain for the recipient of the act, C is the fitness cost for the individual engaging in the behavior, and r is the coefficient of relatedness between them (reflecting the probability that an allele in one of the individuals is present in the other, having been inherited in both from a recent common ancestor).

There is a vast literature describing evidence for kin selection across a wide range of species, including insects (Richards et al., 2005; Nonacs & Reeve, 1995), crustaceans (Duffy et al., 2002), amphibians (Pfennig et al., 1999), fish (Griffiths & Armstrong, 2002), birds (Anderson & Ricklefs, 1995; Krakauer, 2005; Emlen & Wrege, 1988), monkeys (Lee, 1987; Fairbanks, 1990), and plants (Bawa, 2016). Recently, Levy and Lo (2022) found strong support for this rule in an experiment involving financial transactions among human subjects with varying degrees of genetic relatedness.

3.4.2 Group selection

Group selection, whereby an individual incurs a cost to help others in the group, is another route to evolutionary success, and thus another biological explanation for apparently altruistic actions. In group selection, an individual incurs a cost to help their group-mates, some of whom share the genes to produce the behavior.

In modern versions of group selection, the altruistic act toward the group can only evolve by natural selection under specific conditions, for which the genes that influence the action increase in frequency.

The underlying logic of modern group selection is the same as that of kin selection. Selection favors costly acts that benefit other genetically-related individuals enough that the gene in focus increases its frequency in the population (see Marshall, 2011, for a discussion of the equivalence of kin selection and this view of group selection).

There is no debate over the math of group selection. Under very specific conditions, sacrificing for the good of the group can evolve. There is a significant debate, however, as to whether group selection has played an important role in human behavior, and shaping of human psychology. Some argue in favor of group selection being important for people (Bowles & Gintis, 2004; Nowak et al., 2010; Wilson, 1975), while others argue that group selection has not played an important role in shaping human nature (Abbot et al., 2011; Burnham & Johnson, 2005; West et al., 2007b).

3.4.3 Rational spite

Finally, "rational spite" describes actions that are bad for the individual and bad for others. In this case the amount of harm inflicted on the recipient must be sufficiently large that the spite gene increases in frequency. We discussed rational spite in more depth in Ordinaries 11 (Burnham & Phelan, 2023a).

W.D. Hamilton discusses spite as follows, "Would we ever expect an animal to be ready to harm itself in order to harm another more? Such behavior could be called spite" (Hamilton, 1970, p. 1218). Hamilton answered his own question with yes.

Under certain conditions, spite can evolve. The key condition being that the spiteful gene must increase in percentage terms within the population made smaller by the spiteful act. (For more recent work on spite, see Gardner & West, 2004; Gardner et al., 2004; Smead & Forber, 2013).

3.5 Summary of biological explanations for apparent spite and apparent altruism

Natural selection favors behaviors that increase the frequency of alleles (versions of genes) that influence those behaviors. Consider the Belding's ground squirrel, which is preyed upon by hawks. An individual squirrel that sees a hawk can produce an audible alarm. Such an alarm decreases the chance the other squirrels will be eaten, but increases the chance that the alarm caller dies.

Why are Belding's ground squirrels apparently altruistic in making alarm calls? The answer is kin selection. (Recall J.B.S. Haldane's claim that he would die for 8 cousins.) Belding's ground squirrels make the alarm calls when the genetic benefit exceeds the genetic cost. The squirrels do a subconscious mathematical analysis and sound the alarm when it is in the interest of that squirrel's genes that produce the alarm. Here's how it plays out.

Because male squirrels leave the colony, dispersing to another colony at maturity, they have few relatives within close proximity — typically just their offspring and grand-offspring. Because female squirrels remain in their natal territory, they have significantly more relatives nearby — such as siblings, cousins, parents, grandparents, offspring, grand-offspring, etc.

A consequence of this difference in the expected number of genetic relatives who will benefit from hearing an alarm call, is that the vast majority of alarm calls are made by older females (Sherman, 1977). Belding's ground squirrel alarms are *apparently* altruistic, but their apparently altruistic behavior arose through natural selection because the alarm calls benefit underlying genes.

The same logic explains another apparent paradox — this time in human apparent altruism. As we explain in more detail in the next section, Ache hunters bring home meat that is shared equally between the hunter's family and other individuals. There is no obvious repayment for this food sharing. As we will see, there are, however, long-term benefits to the families and children of generous hunters.

Every type of costly behavior that arose by natural selection did so because of one of these two routes. First, the cost of the behavior is more than repaid, on average, by modifying future behavior. Second, the individual is actually sacrificing, not for other organisms, but for the genes that the actor shares with one or more other individuals (see Table 3).

In real situations, of course, these different mechanisms can intertwine. Siblings might be generous with each other because they share 50% of their genes. However, siblings might also keep track of favors and expect repayment. So kin selection and reciprocal altruism often coexist within family relations.

4 Reasons why voluntary acts may not get repaid

4.1 Long and variable repayment

The Ache of South America are a people who lived by foraging (hunting & gathering) into the 20th century (Hill & Hurtado, 2017). Because all humans were foragers up

Table 3 Costly actions benefit selfish genes.(Adapted from Burnham & Johnson, 2005)

		When does the Benefit Redound?	
		Now	Future
To what does the benefit redound?	Gene (at the *expense* of the individual)	• Kin Selection • Group Selection • Rational Spite	Costly behavior that does not increase allele frequency (Does not evolve by natural selection)
	Gene (via the *success* of the individual)	Behavior that helps the organism immediately (no puzzle)	• Reciprocal Altruism • Indirect Reciprocity • Costly Signaling

until the invention of agriculture and animal husbandry, modern foragers such as the Ache have been studied in the hope of learning more about our ancestors.

Among the Ache, there is a much-discussed act of apparent altruism. Ache hunters share their game relatively equally; the children of successful hunters eat no more of a kill than other children. Furthermore, hunting is dangerous, and men are not infrequently killed while hunting. Finally, the best hunters who produce the most calories per hour also tend to work the most, bringing in vast amounts of food (Kaplan & Hill, 1985a).

Why do Ache hunters work so hard, and face death, to feed other people's children? This topic has been the subject of intense debate within anthropology, and there is no definitive resolution. For our purposes, however, there is an illuminating explanation of this apparently altruistic behavior.

One explanation for the apparent altruism of Ache hunters is a much-delayed and probabilistic repayment. Hilly Kaplan and Kim Hill write that "sons of high producers might obtain skills and friendships that other youths do not" (Kaplan & Hill, 1985b, p.237).

Sons of apparent altruists, according to Kaplan and Hill, occasionally receive extremely important benefits as a consequence of the food donations of their fathers. To the extent that this is exemplary, it points out the long and variable nature of repayment. The sons must be old enough to hunt, often more than a decade after some initial hunting and subsequent food donation by their fathers.

So from the perspective of any short time frame — or even years — an act may appear altruistic, but actually may be repaid much later. Furthermore, many hunters will never get repaid through this route. Some hunters will never have a son who becomes a youthful hunter. The hunter may only have daughters, or only daughters that survive; the hunter himself might be killed before having children.

Many apparently altruistic acts may have delayed repayment that is only repaid in some cases. Such acts, however, still may be favored by natural selection. It simply depends upon the *average* payoff of the behavior, not the outcome of any one action.

There is evidence that the children of good hunters do obtain more help from other community members and are more likely to survive (Kaplan & Hill, 1985a). So the apparently altruistic food donations and the hard work of great hunters may be a completely self-interested way of helping their children (and their own evolutionary fitness). It can be viewed as a long-term care insurance policy with payment up front in the form of donated pounds of peccary flesh.

Delayed and probabilistic reciprocity will often appear to be altruistic. The 'altruist' takes a costly action that benefits one or more recipients. The repayment may occur decades later, and many such individual actions may never be repaid.

4.2 Parasitism

Brown-headed Cowbirds (*Molothrus ater*) may be the worst parents on the planet; adult males and females do not know how to take care of their young. Furthermore, Brown-headed Cowbirds do not even sit on their eggs; as soon as the female lays eggs, she abandons her offspring — sometimes flying away in less than a minute.

The Brown-headed Cowbird must rely upon apparent altruism for the rearing of their offspring. The only route of survival for baby cowbirds is being protected and provisioned by the adults of different bird species (Robert & Sorci, 2001). Every single Brown-headed Cowbird egg and hatchling depends on the kindness of strangers to survive.

Finally, as noted, these adoptive parents are not even from the same species! What do the baby cowbirds give back to their foster parents? Nothing. In fact, baby cowbirds sometimes kill the offspring of their host families and always impose costs on the host family by eating food and wearing out the parents (Lorenzana & Sealy, 1997).

Host care of Brown-headed Cowbirds satisfies W.D. Hamilton's definition of altruism. The feeding behavior is costly to the host species and benefits a recipient. Furthermore, because the 'altruist' never gets repaid and the organisms are from different species, none of the explanations for apparent altruism seem to apply.

What is the explanation? Are the hosts being altruists? **Absolutely not.**

Brown-headed Cowbirds are labeled 'brood parasites.' They lay their eggs in the nests of birds of other species and rely upon the neurologic mechanisms of the parasitized host to care for their offspring. Brown-headed Cowbirds are 'obligate' brood parasites, which means that they have lost the ability to care for their own offspring. They are obligated to find a host to take care of their offspring.

Brood parasitism is a well-studied phenomenon in birds, fish, and insects (Sless et al., 2023). Brood parasitism fits the formal definition of altruism in being costly to the actor and beneficial to the recipient. However, brood parasitism is no more 'altruistic' in intent or evolutionary history than when a person gets malaria from a mosquito bite, while the mosquito obtains a nutritious blood meal.

Brood parasites exploit the biological mechanisms of their hosts. Parents of the host species have evolved behaviors to take care of their young. The adult birds' mechanisms rely upon specific environmental cues to trigger specific behaviors. If there is an egg in your nest, keep it warm. If there is a baby bird in your nest chirping "I am hungry," get it food, etc.

We can look across various species to reveal that hosts and brood parasites are in an arms race — an evolutionary battle — in which the hosts seek to minimize the negative impact of the parasites, while the parasites seek to continue fooling the hosts. Hosts use egg traits to find and destroy parasitic eggs including size, color, location, and number (Honza & Cherry, 2017). And these host systems to detect and decrease parasitism, in turn, act as a selective force on the parasites to evolve ever-better ways to fool the hosts.

Brood parasitism is apparent altruism, but it is not an effort by the host to help the offspring of other organisms. It is a co-evolutionary arms race where hosts are under pressure to rid themselves of parasitic costs, and parasites are under selective pressure to retain their ability to obtain benefits from hosts (Takasu, 1998).

4.3 Mismatch

Mismatch is the idea that an organism (or entire populations of organisms) can be out of sync with its environment (See *Mean Genes* [Burnham & Phelan, 2000], [Burnham, 2016], Ordinaries 2 [Burnham & Phelan, 2020a], and Ordinaries 8 [Burnham & Phelan, 2022a] for some of our writing on mismatch). Astronauts in space need to learn how to safely urinate in zero-gravity, but they also need to be taught how to sleep.

Turtles get killed by artificial light. Primates in zoos are fat. And monkeys with access to cocaine and other drugs overdose and die. (See Ordinaries 8, Burnham & Phelan, 2022a, in particular, for detailed mechanistic explanations of these examples of mismatch in sea turtles and primates.)

Behavior is the product of biology and environment. Animals in novel environments exhibit apparently puzzling, and frequently self-destructive, behaviors.

Humans are mismatched to modern, urban environments. This mismatch is the cause of a wide-variety of human phenomena, including obesity, drug addiction, excessive gambling, and some of the apparent spite and apparent altruism that commonly occur.

For our foraging ancestors, the vast majority of their interactions were with people they would see again many, many times. As such, natural selection favored the evolution of reputation-management machinery that implicitly assumes a high probability of repeated interaction. Additionally, behavior was frequently observed and had broad reputational consequences. In contrast, in today's urban settings, many — or even most — of our interactions are with people we will never see again.

Population density is a key parameter for understanding the likelihood of repeated interaction. In large, densely-populated settings, opportunities for one-time and somewhat-anonymous interactions are plentiful. In contrast, in small, sparsely-populated settings (particularly with low mobility), everyone knows everyone else, and reputations are constantly being assessed and updated.

How dense were human societies before the invention of agriculture? Various techniques for estimating population density have been developed. One approach that yields among the highest estimates is 0.19 people per square kilometer (Zhu et al., 2021); see Table 4.

The Chaoyang district in Beijing is 471 square kilometers, which would contain 89 people at hunter-gatherer density of 0.19 people per square kilometer. In 2022, the population of Chaoyang was 3,545,000 (Chinese Economic Database, 2022). The island of Manhattan is 59 square kilometers. At hunter-gatherer density, it would contain 11 people. In 2020, Manhattan had a population of 1,694,000 (U.S. Census, 2020). Table 4 contrasts pre-agriculture and current population densities and sizes.

Human and non-human ancestors lived in low population density for millions of years — up until the very recent (from an evolutionary perspective) invention of agriculture. In low population density environments, the vast majority of behavior is embedded within a context of long-term relationships. As such, individuals are built to account for both the immediate impact of a decision as well as the future impact over many years.

Table 4 Industrialized city densities dramatically exceed those of hunter-gatherer societies

	Size km^2	h/g density individuals/km^2	Population assuming h/g density	Current density/km^2	Current population
Chaoyang district of Beijing	471	0.19	89 people	7,530	3,545,000
Manhattan island	59	0.19	11 people	28,154	1,694,000

Mismatch is the general phenomenon of an organism being out of sync with its environment. Under conditions of mismatch, biological mechanisms that arose to maximize genetic replication produce anomalous behaviors. High population density and increased anonymity are key aspects of mismatch between human genes and our modern environments.

5 Biological economic views of altruism

Modern urban life is filled with costly, voluntary actions that appear to be spiteful or altruistic. Biology has very specific explanations for these behaviors.

Evolution by natural selection favors genetic selfishness. Costly acts that do not redound to the benefit of underlying genes did not arise by natural selection. However, behavior is produced by biological mechanisms interacting with the environment. And so, in some settings, these mechanisms can (reliably and inappropriately) produce behaviors that do not appear to, or actually do not, redound to the benefit of the underlying genes.

We believe that mismatch is the major cause of apparent spite and apparent altruism in modern human behavior. We are built to constantly care about our reputations, even in situations where reputations are not being impacted, or at least much less so than we are built to estimate.

How does biology improve the economics of interpersonal preferences? First, it explains the existing data. Second, it provides a path forward.

5.1 End the debate about 'interpersonal preferences'

Neoclassical economics is built on a wholly-selfish version of human nature. In the neoclassical view, people will never be spiteful (incur unrepaid costs to harm others) nor altruistic (incur unrepaid costs to help others).

In sharp contrast, behavioral economics documents both apparent spite and apparent altruism. Richard Thaler quips that "people are nicer (and dumber) than assumed by neoclassical economics." The word 'nicer' implies some altruistic intent.

Are humans selfish, spiteful, or altruistic? The answer is that the impact of human behavior varies depending on the circumstances. In ancestral settings, the only behaviors favored by natural selection were selfish, in the sense of benefiting that organism's genes. In evolutionarily novel settings such as cities, however, people will often incur costs that are never repaid. In modern settings, people may appear spiteful or appear altruistic.

So the first contribution of biology to the economics of interpersonal preferences is to suggest that both neoclassical and behavioral economics stop arguing over whether people are selfish or 'nicer.' Humans are both apparently spiteful and apparently altruistic depending on the situation.

5.2 Mismatch is central to apparent spite and apparent altruism

Why are humans sometimes selfish and sometimes not? The most important answer is mismatch. Humans evolved in a world where almost all interactions had reputational consequences. Thus, we are built to maintain our reputations. Keeping our good name requires us to help people in some circumstances and to defend our honor in others.

The powerful emotions that regulate human social behavior evolved in small-scale societies with no, or extremely limited, anonymity. Our social emotions are mismatched to modern, dense populations that provide some level of anonymity and include many interactions that are not repeated.

Group size is one of the key features that differentiate modern life from that of our human forager ancestors. Foragers are estimated to have lived in groups that ranged from a dozen people up to about 150 (Kelly, 2013). These groups were fluid, depending, for example, on food availability. Furthermore, these groups were enmeshed within larger communities.

More recently, some scholars argue that sedentary foragers, including communities that fish predominantly, could exceed 1000 people (Singh & Glowacki, 2022). This debate about group size is active within anthropology but not relevant to this paper. Humans evolved in societies massively smaller than modern cities and with little or no anonymity.

In a relatively small-scale society, every person can be important, and reputations are constantly monitored and modified. Consider intrigues in the Roman Senate, which consisted of 300–500 members. In 44 BC, Julius Caesar was famously assassinated in the Senate, by senators including his supposed friend, Brutus.

Just a few years earlier, Caesar and his former-friend-turned-enemy Pompey fought each other in the Roman civil war. Pompey lost the civil war, fleeing to Egypt for refuge. His Egyptian host, King Ptolemy, had Pompey executed and sent his head to Caesar as a gift (Wiseman, 1994).

Roman politics were complicated, subtle, violent, and characterized by fluid coalitions. Here is a scholarly description of Pompey's situation, "It is a well-known fallacy by now to speak as though the Senate were a coherent political party. No Roman politician ever had the whole Senate, or even all the Optimates, on his side. Pompey had friends and enemies, in the Roman sense, like anyone else" (Sherwin-White, 1956, p.7).

Our human emotional structures evolved to help navigate complicated political situations in relatively small groups like the Roman Senate. As described by Robert Trivers, "friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, and some forms of dishonesty and hypocrisy can be explained as important adaptations to regulate the altruistic system" (Trivers, 1971, p.35).

Caesar's Rome was a vast city; the Roman senate was a small society where all the members knew each other, married and murdered people from each other's families, and remembered past actions. Reputations and relationships were central to success and failure for Roman elites.

While the Roman senate was a small-scale society in a large city, our ancestors lived in small groups up until the invention of agriculture. For hunter-gatherers — or anyone in a small-scale society — memories are long, secrets get out, and reputation has important impacts on myriad aspects of life. We have no written records from human societies before the invention of agriculture, but we can look to modern small-scale societies to see the importance of reputation.

Consider the life and death of the Lakota warrior Tȟašúŋke Witkó, known as Crazy Horse (Matson, 2016). For Lakota warriors, indifference to risk in battle was central to obtaining social status.

In 1872, four years before the battle of the Little Big Horn, Crazy Horse took part in a raid against 400 US soldiers. Crazy Horse rode straight at the enemy, showed no outward fear, and had his horse shot out from beneath him. Later, Crazy Horse displayed courage fighting US soldiers in battles such as the Little Big Horn. Because of his fierce and fearless actions, Crazy Horse became a leader of the Lakota.

However, Crazy Horse was subsequently stripped of some of his societal honors. His long-term love was Black Buffalo Woman, who was married to a warrior named No Water. Crazy Horse and Black Buffalo Woman eloped and spent a single night together. No Water tracked the lovers down, shot Crazy Horse in the nose, and broke his jaw. The community elders intervened, judged Crazy Horse to be at fault, and sanctioned him by removing some of his honors and lowering his status.

Reputational issues were central to Lakota life, and Crazy Horse in particular. Leaders were selected based on behavior, particularly the willingness to demonstrate a lack of fear in battle. Furthermore, even leaders were subject to sanction for violation of community norms.

After Crazy Horse eventually surrendered to the US army, he was murdered by a US soldier. A rival Lakota warrior, Red Cloud, was reportedly envious of Crazy Horse, and Red Cloud spread false rumors that contributed to the US army mistrusting and subsequently killing Crazy Horse (Pearson, 2005).

Life in a small-scale society is filled with reputation risk. Undoubtedly, every high school student knows this fact. Show weakness in sports, disloyalty to friends, or make romantic mistakes, and suffer from gossip or worse.

Human beings are built to deal with small-scale society politics. Our emotional structures evolved to help us navigate these risks. No one, of course, is perfect at such maneuvering, as evidenced by the deaths of Pompey, Caesar, and Crazy Horse.

Let us now return to the road rage incident between Darla Jackson and Zach Buob. The two individuals lived in different cities in California's San Diego county. The population of San Diego county at the time of the incident exceeded 3 million people. There is no evidence, from the trial or any other source, that the two individuals had ever met before.

What caused the altercation and death of Zach Buob? In a word, mismatch. Both individuals apparently became furious with each other. Buob kicked Jackson's car and Jackson pleaded guilty to voluntary manslaughter for running over Buob. How is this mismatch?

On a crowded, anonymous California highway, the smart choice is to avoid road rage. Turn the other cheek, drive off, and live to see another day. There is no value in teaching a lesson to someone you have never met before and likely will never see again. If humans had evolved in massive, anonymous societies, it is likely that human emotional structures would be different, and we would not care so much about our interactions with strangers.

Our brains, however, were built for small-scale societies where reputations are extremely important. Thus, we are built to not turn the other cheek but rather to be willing to incur costs to maintain our social standing.

A second aspect of mismatch played a central role in this deadly road rage. Darla Jackson might have gotten very angry in a small-scale society, but she probably would not have been able to kill Buob so easily. Her car, a 20th-century invention, became a weapon. Without such a deadly weapon, and with a bit of time to reflect with some mediators, perhaps the two would have come to a non-violent outcome.

Reputation management is part of the human suite of emotion and behavior. For our ancestors, retaining a good reputation was as important as finding high-quality food and avoiding predation. In some modern settings, our outdated reputational management system causes us to lose money or even lose our lives.

5.3 Biology provides a road forward for economics

Biological mechanisms in situations of mismatch can be the cause of apparent spite and apparent altruism. In small-scale societies, our reputation-management machinery works to the benefit of our genes. In modern settings, we frequently incur costs that are never repaid to either us or to our genes.

How does the biological insight help economics? The answer is two-fold. First, it suggests that most existing work within economics on interpersonal preferences can stop. Second, it provides a framework for novel approaches to engineering outcomes that we might prefer.

On the first point, biological economics tells scholars to stop most of their current work. Neoclassical economics can cease work that assumes people are not impacted by the lives of others. Similarly, behavioral economists can stop efforts that merely document that people can sometimes appear spiteful and at other times appear altruistic. Plato, Adam Smith, and every human who ever lived, knows this truth.

What is the road forward for the economics of interpersonal preferences? Behavior is produced by the combination of biological mechanisms and the environment. And those mechanisms are shaped over thousands of generations of natural selection, maximizing relative reproductive output. If we want to alter the outcome, the only choices are to: (i) alter the environment, or (ii) alter the underlying biology.

5.4 Action item 1: Change the environment to engineer an outcome

Behavior is the product of biological mechanisms and the environment. Route one to changing behavior is to engineer an environment so as to elicit different behavior. One does not need a deep understanding of genetics to use this approach.

Perhaps the most common example is the idea of buying only healthful foods at the grocery store. Engineer your local food environment to nudge your food intake toward something better for you.

Engineering the environment can go beyond folk wisdom. Consider the case of bike theft in a British city. Newcastle University had a problem with bicycle theft. Over a 12-month period, 70 bicycles were stolen; more than one per week.

In an experiment, researchers put posters on the wall near three bicycle racks. The signs contained large images of human eyes and a statement that the bikes were being watched.

In the year prior to the "we are watching you with eyes" sign-posting, 39 bikes were stolen from locations with the signs. In the year after the signs were posted, the number of thefts from these three locations declined to 15.

While the thefts from the "we are watching you" bike racks declined substantially, the overall number of bike thefts in the year after the signs were installed remained largely unchanged; 68 in the period with the signs, 70 in the period without the signs.

The bicycle thieves simply shifted much of their criminal activity away from the bicycle racks with signs toward the racks without signs. The signs did not decrease crime, but more of the crime took place in locations without eye images on nearby walls.

What is going on with these bicycle thieves? And what does it have to do with weighty subjects such as Thomas Kuhn, Charles Darwin, and Adam Smith? First, the story about eye images and human behavior, and then the implications for the economics of apparent altruism and economics more generally.

One of the central causes for apparent spite and apparent altruism is activation of human reputation-management machinery. People tend to act more prosocially in public because they are aware, both consciously and unconsciously, that their reputations are important to their lives.

In short, people are nicer in public than in private because there are rewards to acting nicely. One line of research tests this view by creating experimental situations designed to activate a person's neural architecture for evaluating the level of anonymity.

Up until relatively recently, on an evolutionary timescale, one reliable cue to a lack of anonymity was the presence of human eyes in the environment. If a person could observe an eye (or two) in the environment, this meant that their behavior was being observed.

Natural selection favored the development of neural architecture to specifically detect eyes and other related cues in the environment. This neural architecture is shared across a wide variety of primate species. Humans, and all other primates, have a dedicated neural architecture that detects the presence or absence of eyes, as well as other information such as the direction of gaze of those eyes.

Importantly, this neural architecture is activated not only by actual eyes but also by photographs of eyes. People placed in brain scanners show neural activation to the image of eyes. The literature on neural response to eyes, head orientation, and photographs is summarized in Burnham and Hare (2007).

Thus, the experimental design in the Newcastle bike study used large, human eyes in the posters on the wall. The hypothesis was that because the images of eyes on the poster will activate eye-detection neural machinery, the potential thieves will feel pressure (unconscious or conscious) and move their criminal behavior elsewhere.

In simplified form, the neural architecture for detecting eyes works as follows: If there are eyes in the environment, consider the reputational consequences of actions, along with the direct payoff. One implication is to be nicer when being nice is rewarded socially. However, being in public can also increase the prevalence of apparent spite. It is easier to fail to stand up for oneself if no one is watching.

All of this eye-detection machinery made evolutionary sense for ancestral humans. In a world where reputations matter, natural selection has favored the evolution of a system to alter behavior. When in public, act like a generous hero. When in private, cut some corners and be more selfish.

A variety of experiments report that images of eyes do change the behavior of humans. People give more in a dictator game (Burnham, 2003), give more in a public goods game (Burnham & Hare, 2007), are more likely to pay for their coffee in an 'honor pot' (Bateson et al., 2006), pick up litter (Bateson et al., 2013), and, in Newcastle, steal fewer bicycles from bike racks that are being 'watched' (Nettle et al., 2012).

In fact, one comprehensive review of all the literature on eye cues and behavior, compares the impact of CCTV cameras to that of eye images. Which produces a bigger change of behavior — having the police actually watch you via video, or seeing a photo of eyes?

The answer is that *the ancestral cue of being watched*, is more potent than *actually being watched*! "We report a reduction in the risk of antisocial behaviour of 35% when eye cues are present. By contrast, systematic reviews have suggested CCTV cameras reduce crime by only 16%" (Dear et al., 2019, p 269).

Can we generalize the message from the grocery store and the Newcastle bike racks? Yes. Detailed understanding of the biological mechanisms can help us engineer environments that improve the outcome in large and small ways.

Buying healthful food and putting eye images in the environment have small impacts on behavior, yet robustly demonstrate the concept. Longer-term, the potential is much greater as we learn more about human genetics and physiology.

5.5 Action item 2: Change biological mechanisms to engineer an outcome

Behavior is the product of biological mechanisms and the environment. Route two is to alter the biological mechanism to change behavior.

People have been utilizing no-tech approaches to behavior modification for centuries. A common suggestion, for example, is to eat before you go to the grocery store. Why do we eat? Because eating changes the state of the biological decision-making machinery.

Consider a higher-tech approach to altering biology. Mounjaro (the trade name for tirzepatide) is a drug approved to treat diabetes, that causes incredible weight loss and a host of other positive health changes. A recent study in the *New England Journal of Medicine* reports an average weight loss of 48 pounds or 20.9% for participants who weighed an average of 231 pounds (Jastreboff et al., 2022).

Not only did the average Mounjaro-taking patient lose 48 pounds, but they also had improved blood pressure, fasting insulin levels, and blood lipid levels. Among the patients who were pre-diabetic prior to taking the drug, 95.3% had their blood chemistry returned to normal levels and were no longer classified as pre-diabetic.

Are we telling you to rush out and start taking Mounjaro? No, for two reasons. First, there are a suite of potentially-serious side effects. Second, we don't need to tell you. Mounjaro is going to become the most successful drug in the history of the world — at least until a better drug is invented.

This is a paper on apparent spite and apparent altruism. Why are we writing about weight loss?

Behavior is the product of biological mechanisms and the environment. Ancestral humans faced a persistent problem of too little food and regular famine. Evolution by natural selection produced humans having a ravenous appetite and the ability to store extra calories as body fat. The mechanisms we have for fat storage are adaptations; they evolved because they helped the genes that created them to replicate.

Amazingly effective adaptations for survival and replication have become the leading cause of avoidable sickness and death in our modern environment. How do we get to a better outcome? We have just two options. Change the environment or change the biology. Changing the environment is challenging because pizza purveyors make money by exploiting Pleistocene energy acquisition and storage mechanisms.

Mounjaro illustrates the path of changing the biology. Even in the modern environment of excess calories, people on Mounjaro eat much less because the drug reduces appetite.

Let us return to apparent spite and apparent altruism. Can we change the biological machinery to engineer behavior that we like more? Almost certainly, yes.

6 Concluding thoughts on apparent spite and apparent altruism

In a variety of modern settings, people voluntarily incur costs to hurt other people (apparent spite) or incur costs to help other people (apparent altruism). The mechanisms that produce these behaviors evolved by natural selection to benefit the underlying genes.

In large, relatively anonymous urban environments, many of these costly actions may never redound to the benefit of the genes in the people undertaking the behaviors. Many acts of apparent spite do not help the actors, and, similarly, many acts of apparent altruism are never repaid. The people doing them would have more money, and longer lives, if they refrained from undertaking these actions.

Why do apparent spite and apparent altruism exist? Why do bike thieves avoid bicycle racks with photos of eyes? Why do people enjoy the taste of foods that kill them?

The explanation for these apparently anomalous behaviors is the same, at one level. Ancestral humans evolved neural architectures specifically to win the evolutionary competition — and for no other reason. These neural architectures are adaptations — solutions to problems faced by our ancestors. At the point in time that the underlying genes evolved, they produced behaviors that redounded to the benefit of those genes.

Table 5 Biological Economics of apparent spite and apparent altruism

Phenomenon	Individuals are inconsistent in their attitudes toward other people. People are sometimes spiteful and at other times altruistic.
Neoclassical economics	Individuals care about themselves and derive no pleasure or pain from the lives of others, not even their own children.
Behavioral economics	People are sometimes spiteful in incurring costs to hurt others and sometimes altruistic in incurring costs to help others.
Biological Economics	Natural selection favors maximizing relative reproductive success. Apparent spite and apparent altruism are tools that evolved to further genetic self-interest. In evolutionarily novel settings such as cities, however, people are inconsistent in their attitudes towards others, and often incur costs that are not repaid.

In novel environments, however, these neural systems produce outcomes that redound neither to the material benefit of the individual nor to the replication of their genes. So apparent spite and altruism are the product of naturally-selected mechanisms operating in novel environments (see Table 5).

There are three implications of the biological insights into apparent spite and apparent altruism.

First, economics can alter its focus. We suggest that neoclassical economists stop work that assumes people are selfish in the narrow materialistic sense. Similarly, behavioral economics can stop studies aiming to document that people are not selfish. The current battle within economics regarding the nature of interpersonal preferences is not productive.

Second, we can engineer environments to induce positive outcomes. As a society, we can generalize the "eyes are watching" result. Novel, modern biological tools will enable more detailed physiological understanding that can utilize mechanistic insights to build better worlds.

Third, we can alter biological mechanisms to produce better outcomes. With modern genetic techniques and advanced drug development, this is indeed a brave new world. Are we advocating genetically engineering altruistic people? No. With modern knowledge and insight, however, we will be able to impact the biology that regulates apparent spite and apparent altruism.

Recall that Plato had deep insight into human nature more than two thousand years ago. Darwin elucidated how natural selection shapes organisms' structures, physiology, and behavior fewer than 200 years ago. And we figured out the structure of DNA just 70 years ago. So, these are early days.

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