Journal of Bioeconomics (2023) 25:181–201
https://doi.org/10.1007/s10818-023-09343-9

EDITORIAL

Ordinaries 14: Biological economics

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

Published online: 8 January 2024

Abstract
The *Ordinaries* column began in 2019 to promote a Neo-Darwinian synthesis of neoclassical and behavioral economics. In this, the last Ordinaries article, the goal remains to improve economics by utilizing natural science theory and methodologies to improve economics.

Keywords Economics · Biology · Natural selection · Genetic mismatch · Darwin · Biological economics

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

- Oxford English dictionary.

1 Introduction

This is the fourteenth and last Ordinaries article. In these articles, we argue that human beings evolved by natural selection *and* this fact is important for economics. More than just important — essential. The natural sciences provide a modern — and necessary — foundation for economics.

Today, there is an intellectual divide within economics between neoclassical and behavioral schools. This divide can be healed by theory and data from biology, and the natural sciences broadly. And this realigned perspective will enable economics to move forward with improved accuracy and efficiency.

The schism in economics is summarized as follows:

- Neoclassical economics assumes that people are effortless and nonconscious optimizers of some measure of happiness.
- Behavioral economics catalogs numerous failures of the neoclassical model at describing and predicting actual human behaviors.

✉ 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

Both schools of economic thought lack any unifying, correct framework. Humans are assumed to have a set of attributes, but these attributes are pulled from folk psychology. And because these folk assumptions about human nature are incorrect in important ways, both neoclassical and behavioral economics are fundamentally flawed and circumscribed in their usefulness.

The atheoretic foundation for economics made sense in the 19th and early 20th centuries because the natural science model of behavior was inchoate. This, however, is no longer the case.

During the 20th century, one of the major achievements of biology occurred. Referred to as "The Modern Synthesis," this was the integration of Darwin's ideas about evolution by natural selection with Mendel's discoveries about the mechanisms of heredity, and a mathematical framework based on population-level thinking (Huxley, 1942).

As a consequence of The Modern Synthesis — and the many decades of refinement and elaboration since — evolution became and remains the central organizing principle of biology. It is the lens through which biologists understand and interpret findings across all subfields of the discipline — from paleontology to cell biology to physiology to non-human and human behavior.

We propose a realignment of economics, centered on science's deep understanding that humans, including our behaviors, are the products of natural selection. Based on more than a century of natural sciences research, it has become indisputable that human behavior — including the cellular and physiological mechanisms by which it is produced and regulated — can be best understood from this perspective.

What does biology have to say about economics? A great deal. Natural selection tends to favor optimization, in a manner that resonates with neoclassical assumptions of maximization. But with two significant caveats.

- First, the attribute maximized by natural selection is individuals' relative rate of genetic replication, not happiness.
- Second, behavior is produced by physiological mechanisms that have evolved to be sensitive and responsive to environmental cues. As such, behavior varies and is highly contingent, depending on key features in the environment.

Because behavior is the product of the environment interacting with biology, specific types and rates of changes in the environment will produce systematic failures to maximize. Considered from this perspective, all of the so-called anomalies of behavioral economics are expected and could have been predicted a priori.

Cities and many other modern environments are systematically different from the human ancestral environments to which our genes are adapted. Because we are mismatched to our current environments, modern humans are akin to fish out of water.

In modern, novel-to-our-genes environments, our behaviors no longer automatically maximize anything. Not genetic replication, not lifespan, not happiness, not number of babies, not financial resources. Nothing.

The Ordinaries articles place economics into the larger, modern, natural science framework that covers the behavior of all biological organisms. This framework did not exist when the neoclassical model was developed. Thus, the failures of

neoclassical economics can be viewed as simply a failure to update the model with the discoveries of modern biology.

In contrast, much of the behavioral economic work was produced when biology knew better. Why then didn't behavioral economists utilize the natural sciences? We believe there are two important explanations. First, most economists receive little or no training in the natural sciences. Second, behavioral economists were focused narrowly on critiquing the deeply-flawed neoclassical model.

For historical reasons then, the two main schools of economic thought are fundamentally flawed. There is a productive path forward, however. It is to put a foundation under economic models of human behavior that is derived from the current, much-improved natural science framework.

In *The Structure of Scientific Revolutions*, Kuhn (1962, 1970) argues that paradigm shifts occur in three phases.

> **Phase 1:** An incorrect or incomplete paradigm is prevalent. The neoclassical economic model reflects phase 1 in the Kuhnian framework. It is built on a set of assumptions about human nature that are — sometimes absurdly — inconsistent with actual human nature.
>
> **Phase 2:** Evidence that the existing model is incorrect accumulates. Evidence that does not fit the existing model is labeled 'anomalous' by Kuhn. Richard Thaler's 'anomalies' column in the *Journal of Economic Perspectives* utilized Kuhn's terminology and highlights some of the findings of behavioral economics (Thaler, 1987, and subsequent anomalies articles).
>
> **Phase 3:** A new, better paradigm emerges, which incorporates the correct parts of the original paradigm and synthesizes the anomalies of phase 2.

The natural sciences offer a route to a neo-Darwinian scientific revolution — phase 3 in Kuhn's paradigm — in economics. The Ordinaries column is intended to move economics toward a natural science foundation, with a long-term goal of reuniting and improving economics.

To summarize, the state of economics in the Kuhnian paradigm.

Phase 1: **Neoclassical Economics** - a flawed, dominant paradigm.
Phase 2: **Behavioral Economics** - evidence of flaws ("anomalies") in the dominant paradigm.
Phase 3: **Biological Economics** - a new framework that encompasses and synthesizes the old paradigm (neoclassical economics) and the anomalies (behavioral economics).

To date, we have published thirteen Ordinaries articles (Burnham & Phelan, 2019, 2020a, 2020b, 2020c, 2021a, 2021b, 2021c, 2022a, 2022b, 2022c, 2023a, 2023b, 2023c), each sharing the common goal to attain phase 3 of Kuhn's framework by integrating economics and the natural sciences.

> 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. - Burnham and Phelan (2019)

In this article, we conclude the Ordinaries series. First, we start with three non-technical vignettes that encapsulate our effort to improve economics using biology. Second, we summarize the current schism within economics between neoclassical and behavioral economics. Third, we highlight the key insights from biology that we have utilized and elucidated in this series. Fourth, we summarize what has been accomplished in the series. Fifth, and finally, we discuss the future of biological economics.

2 A non-technical summary of the Ordinaries articles

Here we provide three non-technical discussions that summarize our perspective on economics.

First, neoclassical economics assumes people make perfect decisions, even on novel problems in environments that differ systematically from ancestral settings. The neoclassical economic model has no support in the natural sciences. In fact, the assumption of universal maximization is wholly inconsistent with biological perspectives and observations.

Second, people struggle with self-control, particularly in the area of diet and exercise. Biologists understand exactly why we struggle. This knowledge reliably points toward strategies by which people can improve their outcomes; economists, in contrast, are confused and unhelpful.

Third, the pursuit of "happiness" is unlikely to lead to actually-desirable outcomes, not even happiness.

2.1 Humans are not optimizers in evolutionarily novel situations

Neoclassical economics assumes perfect decision-making. Can anyone who interacts with actual people reasonably believe this view of human nature?

Recently, an extremely well-paid professional (American) football player has been in the news for being penalized repeatedly for making the same mistake over and over. What rule has he been violating that caused the penalties? Is it some subtlety of where to place his hands when blocking? Perhaps the minimum height for a legal "crackback" block?

No. The player has been standing in the wrong location before the play starts. (Technically, these are "pre-snap alignment" violations.)

Every person makes mistakes regularly. We all know this. But when a professional athlete — with guidance from knowledgeable coaches and the ability to study video — makes the same mistake repeatedly, we ought to take notice.

After all, if an expert can make mistakes, even with optimal training and under ideal conditions, why should we imagine that Aunt Joan will be able to price a retirement

annuity accurately? In the face of human fallibility, how can the neoclassical economic model assume perfection?

Here are two of the standard defenses.

Defense 1: Humans are naturally good at solving problems. When we first were introduced to the neoclassical view of optimization, our professor threw a candy bar to a student who caught (and then ate) the candy bar. The professor said, "you did not solve the equations of motion to catch the candy bar. Nor do you need to explicitly calculate anything to save enough money for retirement."

Defense 2: Humans can, with extensive practice, become good at solving problems. Milton Friedman argues that an expert billiards player makes shots that are so precise they appear "as if" the player were solving complicated mathematical equations.

So these defenses are similar. In the physical realm, it is indeed true that humans sometimes behave 'as if' they have solved complicated mathematical problems — problems as complex as the calculations assumed in neoclassical economic models of optimal behavior.

The biological view is as follows. Natural selection favors behaviors that lead to maximum genetic replication relative to the other individuals within the population. People can catch candy bars because for the entire history of humans' existence on earth, objects have obeyed the laws of motion and that has mattered to our survival.

Thus, organisms that could effectively predict movement, say of predators or of animals that were potential food — at least better than their competitors — came to dominate the planet. We can catch candy bars because the ability to perform similar behaviors led to relatively higher genetic replication among our ancestors.

The 'expert' billiards player is a nonsensical argument because it is a learned behavior for a very specific set of situations. Yet the neoclassical economic model assumes perfect decision-making *even for problems never seen before by humans* on the planet (including, for example, "how do I get my new wifi router to connect to the internet?") Novice billiards players, not surprisingly, maximize nothing, and behave "as if" they cannot solve the required equations.

Humans make mistakes all the time. This is not the case, however, when it comes to addressing problems that (a) have been around for a long, long time (such as dealing with gravity), and (b) have an impact on our relative rate of genetic replication.

We are exceptionally good at solving problems that align well with important situations faced by our ancestors. However, people are not naturally expert at solving other types of problems, including playing billiards, installing computer routers, controlling our consumption of novel drugs, avoiding Big Macs, or navigating the modern world.

In summary, neoclassical economics is wrong to assume that people unconsciously and automatically make good decisions. Plato wrote about these aspects of human behavior more than 2000 years before behavioral economics made the same point.

In summary:

Neoclassical Economics: People naturally optimize all decisions.
Behavioral Economics: Neoclassical economics is wrong (see Plato for well-written analysis).

Biological Economics: People are very good at dealing with certain problems that were relevant and important to us in the environmental conditions to which our ancestors became adapted. For example, we are good at dealing with gravity. People are not, however, naturally good in situations that do not line up well with ancestral conditions.

2.2 Diet and exercise

The top three new year's resolutions for 2023 were: Exercise more, eat healthier, and lose weight (Buchholz, 2022). A record percentage, 41%, of Americans now feel they are overweight (Brennan, 2022). How does economics reconcile the discipline's core assumptions with the observation of ubiquitous, voluntary behaviors that create unhappiness?

The neoclassical economist argues that, for those people who are overweight and sedentary, the situation is optimal — even when it hastens disease and death. By neoclassical assumption, each person always chooses perfectly. Thus, choosing to eat a Big Mac must be optimal for that person at that moment.

The consequences of being overweight and sedentary include: diabetes, atherosclerosis, polycystic ovary syndrome, emphysema, high blood pressure, chronic kidney disease, stroke, gout, cancer, osteoarthritis, heart disease, and skin hyperpigmentation.

To the neoclassical economist, these negative health consequences are simply the payment for feeling great when we eat. Complaining about disease and premature death, after a life consuming sugar and saturated fats, is a form of buyer's remorse.

The behavioral economist, in sharp contrast, argues that people are indeed making poor diet and lifestyle decisions. This occurs, they argue, because people are filled with biases and heuristics, and are influenced by culture to make self-destructive choices. The behavioral economics solution is to nudge people toward better choices. For example, add nutrition labels or encourage use of an app that helps count calories.

Here is the biological economic view. Behavior is the product of biological mechanisms and the environment. We have trouble with diet and exercise because our biology is out of sync with the modern environment.

Our biological mechanisms were selected over evolutionary time. Up until recently, our ancestors faced the chronic problem not of obesity, but of *starving* from not having access to sufficient food. As a result of this significant cause of morbidity and mortality, over thousands of generations our ancestors evolved the adaptive capacity to effectively store surplus calories as body fat.

We are built to acquire and store extra energy because we are the descendants of those people who acquired and stored extra energy most effectively, and thereby outreplicated their competitors. This adaptation is a fundamental component of humans' evolutionary persistence.

In the human ancestral setting, our tastes and appetites directed us to good health decisions. Recall that, at least up until the introduction of motors and processed foods, for example, the Tsimane people of the Amazon had "the healthiest hearts on earth." In an environment that resembles that of our evolutionary ancestors, certain aspects of good health come naturally. People make good diet and exercise choices, without the need for any product labels, calorie counting apps, or nudges.

So hunger and the ability to store fat are adaptations that arose and increased in frequency in populations over time due to natural selection. Somewhat depressing, however, is the fact that the very same biology takes us to unnecessarily early death, when it exists in a different environment.

Ironically, the different environment that is so problematic for humans' hunter-gatherer biology is today's novel world, filled with energy-saving machines, agriculture, and industrial production and distribution systems that ensure reliable and abundant sources of food.

What are the implications of the biological economic view?

First, some particular novel foods are simply toxic. Trans fats are an excellent example; they bind to chemical receptors in our taste buds to cause dopamine release in the brain. Moreover, they are cheaper to utilize for companies than other fats, and humans cannot distinguish their taste from that of more-healthful fats.

Without intervention, the world would be (and for much of the past half-century was) filled with trans fats. Trans fats have now been banned in many countries (including the U.S.), and this is good for public health.

Second, there are only two routes to changing behavior. One is to change the environment. The other is to change the underlying biology.

Changing the environment can include banning unhealthful foods or implementing tweaks such as requiring nutrition labels, paying to join a gym, mandatory savings plans, and the full suite of standard approaches. More successful and enduring behavioral changes, however, are likely to result from changing the biology. Novel weight loss drugs are an example, and we expect there to be more and better ways to modify our biology in the future.

In summary:

Neoclassical Economics: Leave people alone. Let us enjoy our Big Macs, sickness, and premature deaths. We know what we are doing and we rationally choose to die.
Behavioral Economics: Nudge people toward consuming foods that are more healthful and engaging in more physical activity.
Biological Economics: Energetic efficiency and hunger are adaptations that arose by natural selection to foster genetic replication over our evolutionary history. Modern problems arise from the interaction between Pleistocene biology and Holocene technology. Solutions are possible by engineering a different environment or changing our underlying biology.

2.3 Hedonism is not satisfying

We once asked the eminent Harvard biologist E.O. Wilson the following question, "Does it ever bother you that honesty, trust, and friendship are nothing more than genetic creations that evolved to maximize replication?"

Before we share E.O.'s response, consider your own thoughts on this question. Are human emotional structures the product of evolution by natural selection? (If not, be prepared to explain what they do arise from.) Is kindness toward our friends and family selfish in a genetic evolutionary sense?

For many, it is challenging — even in the absence of any reasonable alternative — to accept that many aspects of human feelings and behavior have been shaped by evolution solely to favor genetic evolutionary replication. It can be disquieting, even disturbing, to learn that you are being tricked and manipulated by your own genes.

Honestly, we don't remember what we expected E.O. to say. Perhaps some soppy mishmash about doing good in the world.

Instead, E.O. said, "That's where Stoicism comes in." He then turned around at his desk and picked up a photo autographed to him by Admiral James Stockdale.

Admiral Stockdale was a U.S. Navy pilot who was captured and held in a North Vietnamese prison, where he was systematically tortured over more than seven years. After returning to the U.S., he studied Stoicism at Stanford. He and E.O. Wilson became friends, and Stockdale had given E.O. the signed photo as a gift.

Here is our view of the economic relevance of E.O.'s statement, "That's where Stoicism comes in."

Preferences are paramount in both neoclassical and behavioral economics. Life's goal for an individual — in both neoclassical and behavioral economics — is to maximize happiness. The two warring intellectual factions simply disagree about whether humans are effective at achieving their goal.

The neoclassical economist assumes that all decisions are optimal, even if they appear self-destructive. Suicide, opiate addiction, death at age 30 from eating too much? All are examples of utility maximization to a neoclassical economist. Well done.

The behavioral economist, too, considers no higher goal for an individual than hedonism, but believes that people need help to climb the dopamine mountain most effectively. Because people are systematically incompetent, according to the behavioral economist, they must be nudged and guided down the path to pleasure. Left to their own decision-making, people will experience less dopamine stimulation — and the pleasure it generates — than possible.

The Stoic rejects pleasure as the goal of life. E.O. Wilson understood that happiness is nothing but an ephemeral, genetic incentive system, created and shaped by evolution for its effectiveness at motivating individuals to behave in ways that maximize their relative rate of genetic replication.

So, because honesty, trust, and friendship are genetic creations for enhancing relative reproductive success, we individuals are free to try (though it is not easy) to make decisions that generate reduced amounts of dopamine/happiness. Influenced by E.O., this is the final paragraph that we wrote in *Mean Genes* (Burnham & Phelan, 2000):

> Our temptations are powerful and persistent, but we are not destined to succumb. Ancient and selfish, our mean genes influence us every day in almost every way. But because we can predict their influence, self-knowledge plus discipline can provide a winning strategy in the battle to lead satisfying and moral lives.

In summary:

Neoclassical Economics: Life's goal is to maximize pleasure; it will happen automatically. Everything is perfect.
Behavioral Economics: Life's goal is to maximize pleasure; it will not happen automatically.

Biological Economics: Life's goal is not necessarily pleasure; nothing good will happen automatically. A 'satisfying and moral life' requires self-knowledge about navigating the world with an ancient and outdated behavior-generating psychology.

3 Economics without the natural sciences

Economics is currently divided into neoclassical and behavioral schools. These competing perspectives disagree about the axioms of the field. Because the disagreement is focused on the very foundation of the field — the axioms — even the most important conclusions of economics are unsettled.

Is free trade good? If neoclassical economic views of human nature are accurate, the answer is yes. If, on the other hand, behavioral economic views of human nature are correct, the neoclassical 'proof' that free trade is good no longer applies.

The same situation applies to all the theoretical theorems of neoclassical economics. Should we believe in the First and Second Fundamental Welfare theorems? Should we believe in Arrow's impossibility theorem? If neoclassical assumptions about humans are correct: Yes. If economics does not capture true human nature: No.

Assumptions about human nature are — and must be — the foundation of economics. The efficacy of the entire field rests upon these axioms accurately describing human wants and choices. There is a sharp conflict, however, regarding these assumptions. As such, economics rests on an unstable foundation; meaningful progress continues to be hindered by a pervasive lack of consensus across the most important issues.

The four axioms of economics relate to attitudes towards goods, time, risk, and other people. Table 1 summarizes the differing neoclassical and behavioral beliefs relating to these four core issues. Across all areas, neoclassical theory assumes optimality. Behavioral economics, in contrast, recognizes and documents stark deviations from canonical predictions of optimality, labeling the deviations 'anomalies.'

"An empirical result is anomalous if it is difficult to 'rationalize,' or if implausible assumptions are necessary to explain it within the [neoclassical] paradigm" (Thaler, 1987, p. 198). See Ordinaries 1 for a more complete description of the schism within economics over preferences for goods, time, risk, and other people (Burnham & Phelan, 2019). The following summary is adapted from Ordinaries 7 (Burnham & Phelan, 2021c).

The disagreement between the neoclassical and behavioral schools extends far beyond attitudes toward goods, time, risk, and people. The anomalies of behavioral economics also give rise to problematic issues spanning a wide variety of additional topics. Let us consider three of those topics:

Decision-making. Neoclassical economics assumes people make great decisions. Individuals choose the best feasible option, constrained only by money and information. Behavioral economics, in contrast, argues and documents that in a wide variety of situations people use non-optimal decision processes that produce suboptimal choices.

Self-improvement. Neoclassical economics assumes all decisions are optimal. As such, there is no need for individual self-improvement. In the neoclassical view, better

Table 1 Economics is lost without the natural sciences. Adapted from Burnham (2016) and Burnham and Phelan (2019, 2021c)

	Neoclassical economic view	Behavioral economic view	Open questions
Decision making	Optimal. People maximize utility.	Flawed. People often fail to maximize utility.	Why are people bad at decision-making? Is there a theory to help predict what sort of decisions will be particularly problematic?
Goods	People optimize by picking the best, feasible option.	People make inconsistent and flawed choices.	Why do people get pleasure from some destructive choices? Why do people dislike many behaviors that are constructive?
Risk	People make good, consistent decisions regarding risk.	People make inconsistent decisions regarding risk.	Why are people inconsistent in risky choices? Is there a theory to help predict human behavior in uncertain settings?
Time	People make good, consistent decisions involving multiple time periods.	People make inconsistent decisions involving multiple time periods.	Why are people inconsistent in intertemporal choices? Is there a theory to help predict human behavior in discounting settings?
Selfishness	Individuals care about themselves and derive no pleasure or pain from the lives of others, not even their own children.	Individuals are inconsistent in their attitudes toward other people. People are sometimes spiteful and at other times altruistic.	Why are people sometimes spiteful and sometimes altruistic? Is there a theory to predict people's attitudes toward others?
Self-improvement	None needed.	Nudges.	Is there a framework for self-improvement?
Road forward for economics	Journey is over. Behavior is optimal.	More anomalies, new 'behavioral' preferences, more nudges.	The first behavioral economic studies were conducted in the 1960s. Is there a way to speed up progress?

outcomes are possible only with a larger opportunity set (i.e., more money) and/or better information. From the perspective of behavioral economics, conversely, people can be helped by advice. A famous set of behavioral interventions has been labeled "nudges" (Thaler & Sunstein, 2009).

Improving economics. From the perspective of neoclassical economics, the toolkit for understanding human behavior is complete. There is little work ahead to improve economic theory and none to improve individual outcomes. People make optimal decisions about all aspects of life.

Within behavioral economics, on the other hand, at least three strands of ongoing research are relevant to improving results based on these foundational axioms:

1. Continue efforts to document more 'anomalies' — divergences between actual human behavior and neoclassical predictions about behavior.
2. Create behavioral models that are better aligned with observed human behavior than neoclassical models.
3. Invent new and more effective nudges for improving outcomes.

Despite having a clear path forward, behavioral economics suffers from having no underlying theory. Observations unambiguously reveal biases and heuristics. But why are people like this? Behavioral economics proffers no answer. And because behavioral economics is atheoretic, comprising a loose collection of empirically-derived, hard-to-summarize observations, it is difficult to use to predict behavior.

4 Natural science primer for economists

Here are the five most important findings of the natural sciences relevant to economics. Each is described throughout the Ordinaries articles. After short summaries, we have adapted text from prior Ordinaries below to explain each vital idea in more detail.

Fact 1: Natural selection favors optimization and can produce elegant morphology and behavior. Pick your favorite biological trait: Vision in humans, echolocation in bats, multi-thousand-mile migrations of birds and fish? All are produced by evolution by natural selection. Outcompete your conspecific rivals by being better.

Fact 2: Proximate and ultimate causation. Tinbergen (1963) presented a framework of causation that is central to understanding behavior and its relationship with evolution. The proximate, or mechanistic cause, is the physiological machinery that produces behavior. We eat food because our brain releases pleasure-causing dopamine when we eat. The ultimate cause is the impact on the relative rate of genetic replication, or evolutionary success. We eat food to get energy to survive and reproduce.

Fact 3: The economists' idea of 'utility' is nothing more than a genetic incentive system. Genes are essentially omnipotent, but not omniscient. Genes can hard-wire behaviors, such as heart rate. In most situations, however, genes are more effective by ceding some control.

For example, genes cannot know the location, type, and prevalence of food items that an organism will encounter throughout its life. So rather than program foraging behavior directly, genes produce the desire for food, the ability to navigate the world, and reward the organism with pleasure-causing dopamine for finding and consuming food.

Fact 4: Humans are 'mismatched' or out of sync to current conditions. The modern environment is significantly and systematically different from the human ancestral world. Evolution has not had sufficient time to adapt populations to this new environment.

Fact 5: Owing to mismatch, humans in modern environments rarely, if ever, maximize anything. Not babies, not money, not lifespan, not happiness, nothing. This failure

to optimize is the expected outcome for any organism finding itself in an evolutionarily novel environment.

4.1 Natural selection produces elegant adaptations

A brief primer (adapted from "Ordinaries 1," Burnham & Phelan, 2019, and drawn from Phelan, 2021):

Natural selection is a mechanism by which evolution — descent with modification in a population — occurs. It changes populations whenever there is heritable variation for a trait, and individuals with one version of the trait have greater reproductive success than do individuals possessing a different version of the trait.

Adaptation occurs within populations as a result of natural selection. Adaptation refers both to the process by which populations of organisms become better matched to their environment, and to the specific traits that make an organism more fit.

Examples of adaptations abound (Phelan, 2021). Bats have an extremely accurate type of hearing, echolocation, for navigating and finding food, even in complete darkness. Porcupine quills make porcupines almost impervious to predation. Mosquitoes produce effective chemicals that prevent blood from clotting, enabling them to extract blood (for energy and nutrients) from other animals.

What does natural selection look like in action? Consider how the taste preference for consuming dietary fat evolves. It involves three necessary-and-sufficient steps.

> First, there must be variation between individuals in a population regarding the intensity of pleasure they derive from eating fat (such as is caused, for example, by differences in the shape, and dopamine-binding-efficiency, of dopamine receptors in the brain).
>
> Second, this variation is derived, wholly or in part, from different heritable genetic sequences that are passed from parents to offspring.
>
> Third, this variation in taste preference leads to differential reproductive success (by causing those with stronger fat preferences, for example, to have increased likelihood of surviving a food shortage, owing to greater cellular stores of energy).

Over time, human populations evolved so that people possessed an optimal preference for fat, given its prevalence in their environment and value to people at the time. In this context, "optimum" refers to the preference level that maximizes their relative reproductive output and, consequently, genetic replication.

4.2 Proximate and ultimate causation in Tinbergen's framework

Biology uses a framework that recognizes multiple, complementary categories of explanations for any phenomenon (Tinbergen, 1963, 1968). The following is adapted from "Ordinaries 3," (Burnham & Phelan, 2020b).

Tinbergen's framework includes both 'proximate' and 'ultimate' causes. The proximate level of analysis is a physiological, mechanistic explanation; *how* does something

occur? The ultimate level of analysis is an evolutionary, adaptive explanation for a phenomenon; *why* does something occur?

Consider the phenomenon of bird migration each winter. The proximate cause of these annual treks is the shortening day length, perceived by the optic nerve, gradually altering the rate of release of melatonin by the pineal gland, which, upon crossing some threshold, triggers the behavior of facing south and flying. The avian hippocampus is centrally involved in navigation and geographic orientation (Herold et al., 2019).

The ultimate cause of bird migration lies in enhanced evolutionary payoffs for migrating birds, as measured by rates of survival and reproduction relative to non-migrating birds within a population.

Over evolutionary time, birds that did not migrate south for the winter froze to death or starved. Conversely, birds that did migrate, survived and thrived. All birds in a population today, consequently, must be the descendants of those that migrated — and so carry the versions of genes that induce such behavior.

The proximate and ultimate causes of bird migration, while different, are both correct and complementary. To further explore causation, consider the sex ratio of dogs. If we add up all the births of dogs around the world in a year, the number of male puppies born is very close to the number of female puppies born. The sex ratio in dogs is 1:1. Why?

The proximate cause for the 1:1 canine sex ratio lies in the chromosomes. Individuals with two copies of the X chromosome develop as females. Individuals with one X and one Y chromosome develop as males.

While dogs (and most animals) are diploid, the gametes produced by males and females are haploid, carrying just one copy of each chromosome. All eggs carry one X chromosome, while half of a male's sperm carry an X chromosome and the other half carry a Y chromosome (Beatty, 1970). Because half of dog sperm carry a sex chromosome that results in a female puppy and half carry a sex chromosome that results in a male puppy, the result is a 1:1 sex ratio at birth.

The proximate explanation seems to fully describe the phenomenon. However, there are many other species for which the sex ratio is not 1:1 (Hamilton, 1967). For example, males make up significantly more than half of baby Australian brushtail possums (*Trichosurus vulpecula*) under some conditions. This is true even though these possums utilize the same mechanism as dogs for producing gametes and for sex determination.

To understand the phenomenon more thoroughly, therefore, we need to consider the ultimate explanation for sex ratios. The mathematical solution to the optimal sex ratio, derived from evolutionary payoffs, was produced by Fisher (1930).

Colloquially, Fisher's theorem takes the form of thinking about a gene inside an organism 'trying' to maximize the number of grandchildren it produces. Put another way, how can one version of a gene (an allele) maximize its market share relative to other versions of the gene in subsequent generations.

This measure of the evolutionary success of a version of a gene is called its fitness. Imagine yourself as a gene inside a dog, living in a world that happens to be filled with mostly female dogs. What is likely to lead to a higher number of grand-puppies — producing a male or a female offspring?

The answer is that in a female-dominated population, males are relatively scarce, and so each male, on average, has a higher reproductive payoff than the average female. As a consequence, production of male offspring would be favored in such a population. Conversely, female offspring would be favored in a population with a preponderance of males. And so there is an equilibrium solution: the optimal sex ratio is 1:1, as long as males and females are equally costly (Fisher, 1930). This is the ultimate cause for the observed birth sex ratio in dogs.

Why then are more than half of the Australian brushtail possum babies male in some environments? The ultimate cause of this situation derives from the fact that mothers and daughters live together in tree hole dens, while sons disperse to other communities. When suitable den holes are scarce, cohabitation by daughters negatively impacts both mother and daughter (Jennions et al., 2017).

Fisher predicts the equilibrium 1:1 ratio only when costs to the sexes are equal. If possum daughters 'cost' more because they co-inhabit dens, then there is evolutionary pressure for the sex ratio to be skewed toward sons. Fisher's theory is supported by hundreds of research studies showing adaptive shifts in sex ratios away from 1:1 under certain environmental conditions (Navara, 2018).

The proximate cause of sex ratios, or any biological phenomenon, is not sufficient. As with the phenomenon of bird migration, more complete understanding requires recognition of both proximate and ultimate causation. [Further research on the proximate mechanisms by which brushtail possums produce biased sex ratios indicates that the biases are produced before birth (Johnson & Ritchie, 2002; Isaac et al., 2005). Fishman et al. (2018), observed in another mammalian species that maternal testosterone levels were negatively associated with male-biased sex ratios. As maternal testosterone decreases, they give birth to more females.]

4.3 'Utility' is a genetic incentive scheme

Happiness is a genetic tool evolved to induce biological success. Over evolutionary time, natural selection favors preferences that generate pleasure from behaviors that lead to genetic replication. The following is adapted from "Ordinaries 3, Happiness is a genetic incentive scheme," (Burnham & Phelan, 2020b).

The proximate cause of human happiness is the release of dopamine in the brain's pleasure centers. Dopamine is released in response to unexpectedly good outcomes and is withheld when outcomes fall below expectations.

The ultimate cause of this happiness system lies in its evolutionary function. Natural selection created dopamine and the pleasure-based learning and motivation system to manipulate behavior, so as to increase genetic replication, and not simply to increase happiness. Happiness is simply a means to an end.

The ultimate cause of happiness is the enhancement of the relative rate of genetic replication. Here is a modified excerpt from *Mean Genes* explaining this perspective (Burnham & Phelan, 2000).

> Owners of dog racing facilities have learned how to create exciting contests by using an artificial rabbit. The dogs think they'll soon be feasting on rabbit flesh,

> but they'll never catch their prey. To entertain the customers, the racetrack keeps the rabbit just ahead of the dogs.
>
> Happiness is a tool that our genes use to induce us toward behaviors that benefit them. The rabbit moves to further the interests of the racetrack owner, not the dog. Similarly, we strive towards elusive goals, not for our own happiness, but to further the interests of our genes.
>
> We've been built in such a way that satisfaction cannot be won by accomplishing particular goals nor lost by any setback. Allowing us to rest on our laurels or weep over spilt milk would be a genetic mistake. Our genes don't care about our past achievements, only about continually re-positioning our emotional rabbits to keep us working.

Happiness and unhappiness are tools created by our genes to further their goals. Regardless of our circumstances, our biological mechanisms are built to squeeze the most out of us. We are therefore very attentive to small changes that indicate progress and are almost completely unmoved by anything that we expect.

Though it may seem strange, it is not at all necessary for humans (or other organisms) to be consciously aware that pleasure is an ephemeral incentive system that is shaped by natural selection to produce genetic replication. It's not necessary to have awareness of the ultimate "goal" of any of the genes we carry. We simply pursue behaviors that produce pleasure, and this leads to an increased relative rate of replication. Or at least it did in our ancestral environment.

4.4 Strangers in a strange land. Humans are mismatched to the modern environment

Humans exist in a situation of profound genetic mismatch because we live in a world that is very different from the world of our ancestors, to which we are evolutionarily adapted.

Mismatch is perhaps the most important issue for economics. If humans lived without mismatch, it would be productive — at least as a starting hypothesis — to predict that behavior would maximize both happiness and reproduction.

Genetic mismatch extends to all aspects of industrialized life. "Ordinaries 2" (Burnham & Phelan, 2020a) discusses novel features of modern life, including motorcycles and motorcycle helmets, heroin, dentistry, vaccines, and more. In each case, novel inventions and circumstances produce genetic mismatch and, as a consequence, lead to non-optimal behaviors.

Table 2 focuses on the axioms of economics and details some of the most salient mismatches between ancestral and modern environments. For each axiom, industrialized economies have novel inventions that are not in sync with preferences evolved to produce genetic replication in ancestral environments.

Humans live in an alien environment. There is a mismatch between our modern environment and the environment to which we are adapted.

Table 2 Mismatch impacts every axiom of economics. Adapted from Burnham and Phelan (2020a)

	Human environment before the invention of agriculture	**Industrialized economies**
Products in the environment	Persistent for entire lifetime, relatively slow introduction of novel items.	Rapid product proliferation.
Savings	Fat stored on our body, family assistance, and relationships with friends.	Financial instruments, stocks, bonds, real estate, currency, bitcoin.
Food availability	Variable, unpredictable, and generally limiting.	Overabundance for people with sufficient wealth.
Risk	Physical, biological, and social risks.	Physical, biological, social, and novel financial, technological, and pharmaceutical risks.
Social interactions	Public and repeated, most frequently with same relatively small number of people.	Both anonymous and public. Repeated and one-time interactions with large number of people.

4.5 Humans in modern environments do not maximize

What is the prediction for behavior in an alien environment? Because evolution has not adapted humans to life in modern industrialized societies, no one should expect people to be naturally good at living in cities or other modern settings. And, in fact, no field other than economics does.

Quite to the contrary, organisms can reliably expect to have poor outcomes in novel environments. It is a well-documented and near-universal observation among biologists: if you place an organism in an alien environment, it will experience bad outcomes.

Fish out of water die, orangutans in zoos and rodents in laboratories become morbidly obese; people in space need adult toilet training. Almost nothing comes naturally or functions smoothly in a novel environment (see Burnham (2016) and Burnham and Phelan (2020a) for a fuller explanation).

People living in novel environments struggle to avoid eating too much, to buy the correct financial insurance, to minimize opioid consumption, and to save money. None of our ancestors, who lived before the invention of agriculture, faced these problems. And, as a consequence, humans are able to solve novel problems in novel situations only with significant cognitive effort and training. (And even then, with varying degrees of success.)

5 Economics with the natural sciences

Humans are biological organisms, making decisions using specific neurophysical machinery, shaped by evolution via natural selection. We exist in a profound state of genetic mismatch; the world we live in today differs from our ancestral environment in important and systematic attributes.

Table 3 Biological insights on the road to a Neo-Darwinian economic synthesis. Adapted from Burnham (2016) and Burnham and Phelan (2019, 2021c)

	Neoclassical economic view	Behavioral economic view	Biological Economics
Decision making	Optimal. People maximize utility.	Flawed. People often fail to maximize utility.	Utility is a genetic incentive system selected to induce reproductive success. Genetic mismatch causes people to make decisions that maximize neither happiness nor reproductive success (*Ordinaries 3* & *12*).
Goods	People optimize by picking the best, feasible option.	People make inconsistent and flawed choices.	People live in evolutionary novel environments. Our battle with our own tastes is caused by genetic mismatch (*Ordinaries 1*, *2* & *6*).
Risk	People make good, consistent decisions regarding risk.	People make inconsistent decisions regarding risk.	Natural selection favors optimal risk-taking. Genetic mismatch produces the anomalies documented by behavioral economics (*Ordinaries 2* & *10*).
Time	People make good, consistent decisions involving multiple time periods.	People make inconsistent decisions involving multiple time periods.	Natural selection favors optimal discounting. Genetic mismatch produces the anomalies documented by behavioral economics (*Ordinaries 2*, *3* & *8*).
Selfishness	Individuals care about themselves and derive no pleasure or pain from the lives of others, not even their own children.	Individuals are inconsistent in their attitudes toward other people. People are sometimes spiteful and at other times altruistic.	Natural selection favors maximizing genetic success. People value relatives according to the "coefficient of relatedness." Spite and altruism are tools to further self-interest (*Ordinaries 2*,*10* & *13*).
Self-improvement	None needed.	Nudges.	There are four strategies for self-improvement: will power, innovation, mast strapping, & dopamine modulation (*Ordinaries 4*).
Road forward for economics	Journey is over. Behavior is optimal.	More anomalies, new 'behavioral' preferences, more nudges.	Integration with natural sciences theory and methodology (*Ordinaries 1-14*).

The preceding two sentences are sufficient to provide the core of a synthesis of neoclassical and behavioral economics. Natural selection favors non-conscious optimization of precisely the sort assumed by neoclassical economics. Evolution favors 'as if' maximization of the relative rate of genetic replication.

The selective pressure to maximize evolutionary genetic success is manifest in biological physiology. As such, behavior is never perfect, but at best, it statistically

approximates optimality. In environments different from ancestral environments, behavior is systematically different from what would maximize replication or any other attribute.

An 'ordinary' is something easily predicted and commonplace. Human behavior in modern environments is predicted by biology to fail to maximize. Thus, the deviations from optimality documented by behavioral economics, and labeled as 'anomalies,' are, in fact, the obvious outcomes of naturally-selected biological mechanisms operating in novel environments. This is why we consider the 'anomalies' of behavioral economics to be, in fact, "ordinaries" (see Table 3).

6 Conclusion

Human beings evolved by natural selection *and* this fact is important for economics. Unconnected to the natural sciences, economics is floundering in an incoherent state with divergent camps disputing each and every axiom of the field. The neoclassical economic model assumes optimality; behavioral economics documents the foundational failures in the neoclassical model, but provides no replacement.

6.1 The coming paradigm shift in economics

Thomas Kuhn describes paradigm changes in *The Structure of Scientific Revolutions*. Throughout the Ordinaries articles, we have utilized the Kuhnian framework applied to economics. Phase 1 was the incomplete and inaccurate neoclassical model of human behavior. Phase 2 has consisted of behavioral economics documenting the flaws in the neoclassical paradigm.

Phase 3 is yet to be completed within economics, and, consequently, the field remains in a quiet crisis. In Kuhn's words, the crises caused by the cumulative weight of anomalies can be resolved "only when the paradigm theory has been adjusted so that the anomalous has become the expected" (Kuhn, 1970, p. 53).

In the Ordinaries columns, we argue that the natural sciences provide the perspective that will heal the schism between the neoclassical and behavioral economic schools. Seen in this new light, the behaviors that so puzzle economics are, in Kuhn's words, expected.

In Phase 3, will biological economics incorporate and replace the current fields of neoclassical and behavioral economics? No. At least not in the cohesive manner of some other well-known paradigm shifts.

Two of the best-known examples of scientific revolutions are: 1) the Copernican replacement of the Ptolemaic view of the universe, and 2) The theory of general relativity that includes Newton's laws of motion as a limited case in some situations.

In each of these two cases, the new theory cleanly replaced the prior theory. Ptolemy placed the Earth at the center of the universe. Copernicus, with the Sun at the center of the solar system, completely replaces the Ptolemaic, geocentric model. No remnant of geocentrism remained after the paradigm shift.

Similarly, Newton's work on the laws of motion is a good approximation under certain circumstances. The theory of relativity includes Newton's laws as a special

case, but extends the theory to include situations where Newton's laws alone would be significantly inaccurate.

With Copernicus, there is no need for Ptolemy. With the theory of relativity, there is one theory that encompasses Newton's laws.

Will there be a simple, unifying replacement for neoclassical and behavioral economics? Yes, at a theoretical level. No, at a behavioral level.

Biological economics is not going to produce a model that predicts human behavior in all cases. This may seem disappointing, but, upon even brief reflection, it must be true. Human behavior is incredibly complex and inextricably linked to and influenced by the environment.

Neoclassical economics may be the only field that claims to understand all human behavior — simply by assuming that whatever an individual does is optimal. But neoclassical economics does not describe people in real situations, and no theory will accurately predict human behavior in all circumstances.

Behavior is produced by specific biological machinery that is sensitive to cues from the environment. As such, while there is selection for biological maximization, as long as environments vary, behavior will not be optimal in all situations.

Furthermore, the "optimal" behavior will change along with the environment. Humans around the world today live in evolutionarily novel environments. Animals in novel environments do not maximize anything.

Even when organisms are in sync with their environments, behaviors can be non-optimal for a variety of reasons. Thus, there is not, and there can never be, a simple, cohesive prediction for human behavior. Humans in cities will not maximize utility, nor will they maximize reproductive success.

6.2 Biological economics

What then is the value of biological perspectives on economic behavior?

First, one should never assume that an organism will maximize anything in a novel environment. Humans in modern cities do not maximize happiness, genetic replication, or acquisition of resources. Nothing is maximized consistently or universally in a novel environment.

So the neoclassical assumption of maximization is not correct. Similarly, and consequently, we can discard any notion of societal optimality as the natural outcome of free exchange. The first and second fundamental welfare theorems are not correct (See Ordinaries 11, Burnham & Phelan, 2023a).

Second, to be useful, behavioral economics must accomplish much more than documenting failures of the neoclassical model. The standard behavioral economic formula of assuming optimality and then showing non-optimal behavior is neither interesting nor novel. Because humans cannot be assumed to optimize, mere demonstrations of non-optimality are not productive.

Third, the biological economic perspective argues for a significant change in economic research. Specifically, a majority of the types of economic work that have been done in the past ought to be stopped. What then is there for economics to pursue?

Economists should work to improve outcomes through understanding biological theory and mechanism, as they relate to shaping human behavior. The most fruitful

approach, we believe, is to alter behavior by engineering the environment or altering biological machinery. In Ordinaries 12, we lay out three strategies to decrease genetic mismatch. (See Ordinaries 12: "Return to the Pleistocene" for a full discussion of these techniques.)

- Invent new products that are less toxic than existing vices.
- Invent new products that are less aversive than existing virtues.
- Invent new compounds that alter human physiology to reduce the negative impact of mismatch.

Fourth, as an individual or someone helping craft institutions, utilize three general strategies to achieve long-term goals. (See Ordinaries 4: "Surviving Desire: The Causes and Cures of Self-Control Issues" for a full discussion of these techniques.)

- Use commitment to alter behavior to better align with long-term goals.
- Utilize novel products, as developed by technology or other methods, to align short- and long-term goals.
- Alter the dopamine payoffs associated with behaviors of interest in order to increase or decrease incentives as desired.

Technological innovation holds significant promise for improving outcomes for people. Economists are unlikely to undertake these biological innovations, but they can measure and synthesize such activity, and explore avenues of effective implementation of such innovations.

6.3 Summary thoughts

What will biological economics look like? It will explain behavior as the product of naturally-selected mechanisms operating in particular environments. The existing debates over optimality within economics will disappear. The focus will turn to crafting environments and implementing biological interventions to produce better outcomes for individuals and groups.

The biological synthesis of economics will take decades. Other scientific paradigm shifts, such as the Copernican Revolution, took a similarly long time. Although the path is long, and will extend beyond our lives, we take these steps to promote a new and improved, scientific economics.

References

Beatty, R. A. (1970). The genetics of the mammalian gamete. *Biological Reviews, 45*(1), 73–117.

Brennan B. M. (2022, January 6). What percentage of Americans consider themselves overweight*? Gallup.com*. https://news.gallup.com/poll/388460/percentage-americans-consider-themselves-overweight.aspx

Buchholz, K. (2022, December 23). America's top new year's resolutions for 2023. *Statista Infographics*. https://www.statista.com/chart/29019/most-common-new-years-resolutions-us/

Burnham, T. C. (2016). Economics and evolutionary mismatch: Humans in novel settings do not maximize. *Journal of Bioeconomics, 18*(3), 195–209.

Burnham, T., & Phelan, J. (2000). *Mean genes. From sex to money to food, taming our primal instincts*. Perseus.
Burnham, T. C., & Phelan, J. (2019). Ordinaries 1. Thomas Kuhn, Adam Smith, and Charles Darwin. *Journal of Bioeconomics, 21*(3), 145–155.
Burnham, T. C., & Phelan, J. (2020a). Ordinaries 2. Strangers in a strange land: Mismatch and economics. *Journal of Bioeconomics, 22*(1), 1–11.
Burnham, T. C., & Phelan, J. (2020b). Ordinaries 3. Happiness is a genetic incentive system. *Journal of Bioeconomics, 22*(2), 63–76.
Burnham, T. C., & Phelan, J. (2020c). Ordinaries 4. Surviving desire: The causes and cures of self-control issues. *Journal of Bioeconomics, 22*(3), 137–154.
Burnham, T. C., & Phelan, J. (2021a). Ordinaries 5. Intertemporal choice: Biology informs economic theories of discounting. *Journal of Bioeconomics, 23*(1), 1–14.
Burnham, T. C., & Phelan, J. (2021b). Ordinaries 6. Big Macs & economics: Why we love foods that kill us. *Journal of Bioeconomics, 23*(2), 125–149.
Burnham, T. C., & Phelan, J. (2021c). Ordinaries 7. Toward a neo-Darwinian synthesis of economics. *Journal of Bioeconomics, 23*(3), 225–236.
Burnham, T. C., & Phelan, J. (2022a). Ordinaries 8. Thaler, cashews & Tinbergen: Biological mechanism and behavior. *Journal of Bioeconomics, 24*(1), 1–35.
Burnham, T. C., & Phelan, J. (2022b). Ordinaries 9. How to write a biological economics article. *Journal of Bioeconomics, 24*(2), 117–131.
Burnham, T. C., & Phelan, J. (2022c). Ordinaries 10. Decision under uncertainty: Biology informs economic theories of risk. *Journal of Bioeconomics, 24*(3), 181–202.
Burnham, T. C., & Phelan, J. (2023a). Ordinaries 11. Biological welfare economics. *Journal of Bioeconomics, 25*(1), 1–33.
Burnham, T. C., & Phelan, J. (2023b). Ordinaries 12. Return to the pleistocene. *Journal of Bioeconomics, 25*(2), 75–98.
Burnham, T. C., & Phelan, J. (2023c). Ordinaries 13. Apparent spite & apparent altruism. *Journal of Bioeconomics, 25*(3).
Fisher, R. A. (1930). *The genetical theory of natural selection*. Clarendon Press.
Fishman, R., Vortman, Y., Shanas, U., & Koren, L. (2018). Female-biased sex ratios are associated with higher maternal testosterone levels in nutria (*Myocastor coypus*). *Behavioral Ecology and Sociobiology, 72*, 1–9.
Hamilton, W. D. (1967). Extraordinary sex ratios. *Science, 156*(3774), 477–488.
Herold, C., Schlömer, P., Mafoppa-Fomat, I., Mehlhorn, J., Amunts, K., & Axer, M. (2019). The hippocampus of birds in a view of evolutionary connectomics. *Cortex, 118*, 165–187.
Huxley, J. (1942). *Evolution: The modern synthesis*. Wiley.
Isaac, J. L., Krockenberger, A. K., & Johnson, C. N. (2005). Adaptive sex allocation in relation to life-history in the common brushtail possum, *Trichosurus vulpecula*. *Journal of Animal Ecology, 74*(3), 552–558.
Jennions, M., Székely, T., Beissinger, S. R., & Kappeler, P. M. (2017). Sex ratios. *Current Biology, 27*(16), R790–R792.
Johnson, C. N., & Ritchie, E. G. (2002). Adaptive biases in offspring sex ratios established before birth in a marsupial, the common brushtail possum, *Trichosurus vulpecula*. *Behavioral Ecology, 13*, 653–656.
Kuhn, T. S. (1962). *The structure of scientific revolutions*. University of Chicago Press.
Kuhn, T. S. (1970). *The structure of scientific revolutions* (2nd ed.). University of Chicago Press.
Navara, K. J. (2018). Introduction to vertebrate sex ratio adjustment. *Choosing sexes* (pp. 1–11). Springer.
Phelan, J. (2021). *What is life? A guide to biology, with physiology* (5th ed.). Macmillan.
Thaler, R. H. (1987). Anomalies: The January effect. *Journal of Economic Perspectives, 1*(1), 197–201.
Thaler, R. H., & Sunstein, C. R. (2009). *Nudge: Improving decisions about health, wealth, and happiness*. Penguin.
Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift Für Tierpsychologie, 20*(4), 410–433.
Tinbergen, N. (1968). On war and peace in animals and man: An ethologist's approach to the biology of aggression. *Science, 160*(3835), 1411–1418.