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# TO BEAT OR NOT TO BEAT

Evolutionary processes that shape patterns of behavior in animals and humans can be insightfully described using *game theory* – a mathematical framework initially developed in economics.

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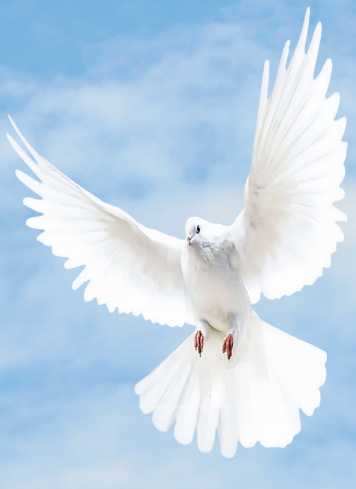
Darwin's theory of evolution stands as one of the most significant theories in modern science, exerting a profound influence on fields as diverse as social sciences and philosophy. Given that modern natural sciences are firmly rooted in mathematics, this raises the question of how evolutionary biology relates to the "queen of sciences."

One of the earliest mathematical models of evolutionary processes was Carl Düsing's model for the evolution of the sex ratio, developed in the late nineteenth century shortly after Darwin's landmark publications. Later, in the 1920s, population genetics was mathematically modeled by pioneers of the neo-Darwinian synthesis, including Ronald A. Fisher, Sewall Wright, and John Haldane. A range of theoretical concepts – including *systems theory*, advanced by Austrian biologist Ludwig von Bertalanffy – have emerged out of biological research. Even *chaos theory*, one of the most revolutionary



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The "hawk" and "dove" strategies illustrate two contrasting behavioral patterns: one that escalates conflict, risking injury or even death (the "cost" in the pursuit of reproductive success), and another that avoids conflict by retreating

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concepts in modern science, partly owes its origins to Robert May's simplified models of population dynamics (alongside the study of weather phenomena).

Evolutionary phenomena have also inspired computer scientists working on optimization methods, such as genetic and evolutionary algorithms, as well as learning algorithms. Evolutionary biology itself gains insights from the exact sciences, frequently employing mathematical tools and computer simulations used in disciplines like physics and even economics. This brings us to the main topic of this article. In evolutionary biology, an essential part of explaining natural phenomena involves calculating the costs and benefits associated with a given trait or behavior. This analysis applies to characteristics like body size, the allocation of energy to reproduction or immune responses, as well as to mating behaviors and the emergence of altruistic behaviors in nature. Many situations observed in nature appear paradoxical; for example, it's not easy to explain why predators are often less aggressive toward one other than rodents are, or why most species display a roughly equal ratio of males to females (as in Düsing's pioneering model). In moments like these, when armchair reasoning alone seems to be leading nowhere, it's time to turn to mathematics.

## Strategy

One of the primary tools for addressing such problems is known as *evolutionary game theory*. This field was developed by John Maynard Smith, a British evolutionary biologist and former aeronautical engineer. It emerged out of methods borrowed from economics, originally formulated by one of history's most renowned mathematicians, John von Neumann, and German economist Oskar Morgenstern, and later expanded upon by John Nash, who was famously portrayed in the film "A Beautiful Mind." This raises an important question: what is a "game" from the mathematical perspective? The answer is straightforward: a game consists of a set of strategies (behavioral patterns) along with functions that assign abstract payoffs to participants based on their chosen actions. To apply this theoretical framework to biological issues, we assume that these strategies represent the behavioral patterns of organisms or other traits that influence the outcomes of their interactions with others, while the payoffs reflect the overall reproductive success of each player.

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The inception of evolutionary game theory is typically considered to be the 1973 publication of the article "The Logic of Animal Conflict" by John Maynard Smith and George Price in the journal *Nature*. They sought to explain the paradox of ritualized conflict among well-armed, predatory animals. This model, now known as the *hawk-dove game*, illustrates that when aggression carries high costs (e.g., increased

Two snakes in combat provide an example of *ritualized conflict*, where rivals avoid true violence and instead try to intimidate each other into retreat. The question of explaining this phenomenon played a role in the development of evolutionary game theory

mortality leading to a significant decline in reproductive success), the proportion of aggressive individuals (metaphorically referred to as "hawks") decreases to a stable level. However, these aggressive individuals do not disappear entirely; the model shows that under favorable conditions, they effectively reduce their own numbers within the population.

## What is more beneficial?

Similar models have been created to explain other seemingly paradoxical phenomena observed in nature, such as the evolution of cooperative behaviors, which utilize frameworks based on the so-called *prisoner's dilemma*. This model, which originated during the Cold War, describes a decision-making conflict regarding a potential nuclear war. In this scenario, two prisoners face a dilemma: betray their partner to receive a reduced sentence or remain silent. If both players choose to stay silent, the punishment is shared equally; however, if one betrays the other, the betrayer receives a lighter sentence while the silent partner faces a harsher penalty. In a single instance of this type of conflict, remaining silent is entirely unprofitable. Yet, when the situation is repeated, the choice becomes more complex, and a strategy known as "tit for tat" (i.e., "an eye for an eye") can emerge. Further research has shown that whether cooperation develops depends on the structure of the population, which influences how individuals interact with one another. In structures that allow for the formation of homogeneous cooperating subgroups, cooperative behaviors may thrive. This is a highly intricate issue, and many studies are being conducted in this area.

Evolutionary game theory is still relatively young, as scientific disciplines go, and is still undergoing rapid development. One of its challenges lies in how to properly interpret concepts borrowed from economics in the context of population processes, which is closely related to the definition of Darwinian fitness. Recent research has focused on increasing the realism of models used in biology and understanding the relationships between natural selection processes and ecological and demographic factors. For instance, methods are being developed to derive payoff functions from demographic models that also account for the life cycles of individuals. This requires increasingly sophisticated mathematical techniques, such as delay differential equations or complex systems of ordinary and partial differential equations. In any case, the discipline is entering a period of intense growth.

It is also important to note that the mathematical techniques and methodologies developed can be applied in other scientific fields, aiding in the creation of more precise models for tumor growth (where evolutionary game theory methods are now being utilized). Pioneering work by Joel Brown has shown that conflicts of interest exist among different types of cancer cells, presenting opportunities to enhance the effectiveness of therapies. Currently, mathematical models are being used in clinical practice to optimize drug administration strategies, significantly improving treatment efficacy. Additionally, methods from evolutionary game theory are being applied to model social and economic processes, such as the evolution of social norms, including cooperation for the common good. This might be seen as biology "repaying" its debt to economics for borrowing game theory. ■


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Further reading:

Poleszczuk J., *Ewolucyjna teoria interakcji społecznych* [Evolutionary Theory of Social Interactions], 2004.

Binmore K., *Game Theory: A Very Short Introduction*, 2007.