Evolutionary Stable Strategy

Application of Nash Equilibrium in Biology

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Every behaviourally responsive animal (including us) make decisions. These can be simple behavioural decisions such as where to feed, what to feed, how long to feed, decisions related to finding, choosing and competing for mates, or simply maintaining ones territory. All these are conflict situations between competing individuals, hence can be best understood using a game theory approach. Using some examples of classical games, we show how evolutionary game theory can help understand behavioural decisions of animals. Game theory (along with its cousin, optimality theory) continues to provide a strong conceptual and theoretical framework to ecologists for understanding the mechanisms by which species coexist.


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Keywords

Evolutionary game theory, evolutionary stable state, conflict, cooperation, biological games.

Most of you, at some point, might have seen two cats fighting. It is often accompanied with the cats facing each other with puffed up fur, arched back, ears back, tail twitching, with snarls, growls, and howls aimed at each other. But, if you notice closely, they often try to avoid physical contact, and spend most of their time in the above-mentioned behavioural displays. Biologists refer to this as a 'limited war' or *conventional* (ritualistic) strategy (not causing serious injury), as opposed to *dangerous* (escalated) strategy (*Figure* 1) [1]. Such behaviours, i.e., avoidance of physical contact in order to minimize chances of injury when fighting for mate or territory, are also seen in other animal groups such as dogs, wolves, as well as humans.

Now allow us to explain a few things about cat behaviour, which will help better understand the *limited war* strategy. All cats (there are 38 species in the world) are territorial animals, and they actively maintain their territories using scent-marking. They mark either using their facial glands, or urine. If you have had a

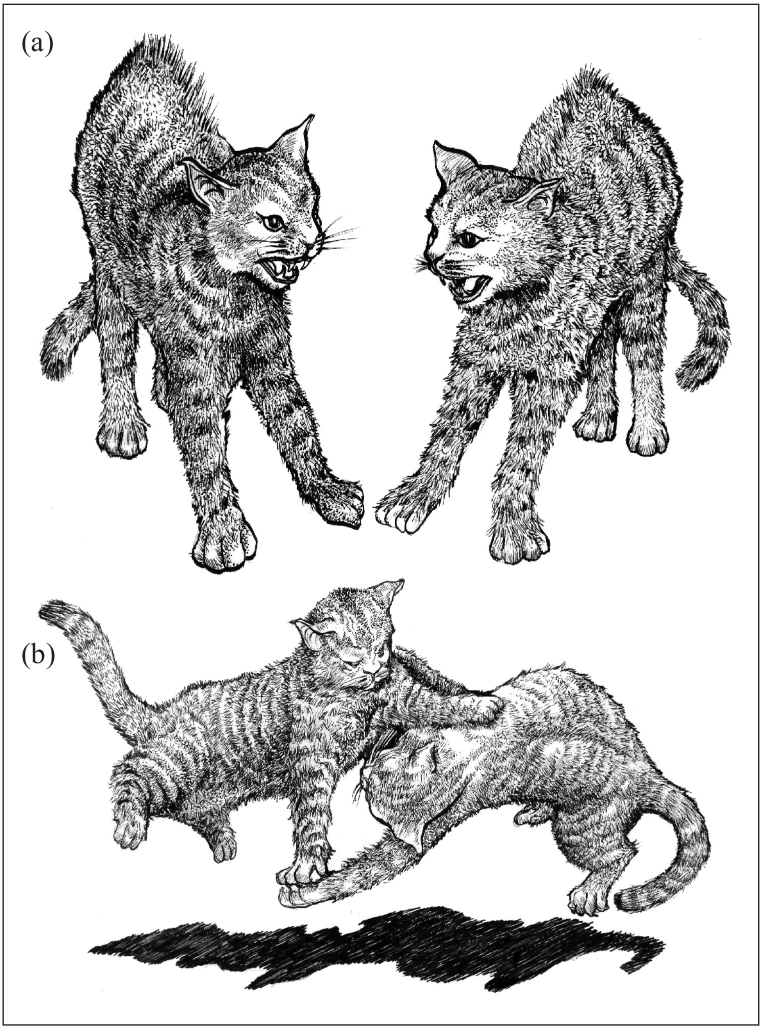

Figure 1. (**a**) Limited war or conventional strategy and (**b**) total-war or dangerous strategy.
Sketch by: Ayan Guha

domestic cat rub its face against your leg, it most likely marked you with excretions from its facial glands. These marking behaviours act as signal to the other cats in that area about its presence (identity). This makes other individuals think twice before intruding, thereby reducing the chances of a conflict. If the intruder decides to ignore these signs, then sooner or later this will lead to a combat. Similar territorial behaviour is seen not only in other predators such as wild dogs, wolves, and mongoose, but also among non-predators such as rhinos and antelopes which form a dung pile or specific spots within their territory where they regularly defecate.

The interaction between the resident cat and the intruding cat can be considered a game. Say ABOL and TABOL are the two male cats (i.e., the players) ready for combat. They being vicious fighters, are capable of inflicting serious injuries to each other. When they meet to fight, both possess a set of strategies (tactic): the less dangerous (no physical contact, but use behaviours mentioned above) or *conventional* strategy '*C*', and a *dangerous* '*D*' strategy (having physical contact) which can likely lead to serious injuries to its opponent, and also itself. So, cats that are only growling and snarling at each other are using '*C*' strategy, and when they inflict wounds on one another (paw fighting) they are using a '*D*' strategy. The interaction between the two cats is a game because the strategy used by ABOL depends on TABOL's strategy and *vice versa*. In most cat-duels the, '*C*' strategy is more common [1].

This interaction between ABOL and TABOL can be explained by a classical game – the *prisoner's dilemma* (*Box* 1), which was first described in the context of two arrested prisoners, being separately interrogated, who have to independently decide whether to confess or deny a crime.

Let us look at the cat interaction using the prisoner's dilemma game. As we mentioned earlier, each individual has two strategies (*conventional* and *dangerous*). The outcome of their

Box 1. Prisoner's Dilemma

Imagine a situation where two individuals have been arrested for a crime they have cooperated to perform. Now they are being questioned separately so that one implicates the other. If neither accuses the other, both are set free – the cooperative strategy.

The police decide to tempt them a bit, so that one or both defect. They give each prisoner the following offer. If one defects against the other, then she is going to be set free (and will also receive a small reward) and the other prisoner is punished. But, if one of the prisoners implicates the other, and not *vice versa*, then the implicated partner gets a harsher sentence. If both confess, both are punished.Each prisoner's dilemma is that, if they both think rationally then the best thing to do is to implicate the other, although they would both be better off trusting each other

Figure 2. A payoff matrix between ABOL and TABOL, which shows that when they alwlays cooperate and plays the conventional '*C*' tactic it is best for everyone (for them and their species) as opposed to '*D*', the dangerous tactic or section fight.

		ABOL (Individual 1)	
TABOL (Individual 2)		***C***	***D***
	C	**LIMITED WAR/ ALWAYS COOPERATE**	ABOL WINS
	D	TABOL WINS	**SERIOUS INJURY/ ALWAYS DEFECT**

interations, can be laid out in a matrix form, i.e., the payoff matrix (*Figure* 2). The best strategy for both ABOL and TABOL is to use strategy *'C'*, i.e., avoid a fight and hence injury, which is an equilibrium payoff, i.e., a Nash equilibrium (both ABOL and TABOL achieve a maximum payoff). In evolutionary terms, it is called an *Evolutionary Stable Strategy* (*ESS*), [1, 2]. In evolutionary game theory, a system is not driven by its players, by the differential success of strategies in a population (described later).

In evolutionary game theory, a system is not driven by its players, rather by the differential success of strategies in a population.

In reality, animal combats are vastly complicated, and this simple game is likely to be played over and over again. In this repeated game, also known as the *iterated prisoner's dilemma* [3], ABOL and TABOL play the prisoners dilemma game multiple times, and each remembers the previous actions of its opponent and changes its strategy accordingly. Let us try to represent their interactions:

ABOL: *C C C C C C C C C D C C C C C C C D*
TABOL: *C C C C C C C C C D C C C C C C C R*

ABOL starts by cooperating (*'C'*), TABOL retaliates with *'C'*. ABOL continues with *'C'* for the first nine moves, but on the 10th move, it decides to play *'D'*, even though TABOL played *'C'* in the earlier move. This 'provocation' escalates their interaction, and TABOL retaliates by playing *'D'*. In the above example, when ABOL provokes in the 18th move, TABOL retreats (*'R'*), and ABOL is the winner! If it was a good territory (lot of food/mate) that they were fighting over, ABOL would have a greater fitness benefit (more number of offspring left behind). All is not bad news for TABOL. Its decision to retreat not only reduced its chances of getting injured, but it also helped save both energy and time, vital resources which could be used in another location (e.g., challenging another individual, or seeking out new feeding grounds) or could be spent on foraging.

Do Bad Guys Always Win: Not True

Animals have been playing games even before humans came along. These games have given rise to multiple coexisting strategies. But all animals have individual variation within a population, which in other words is their personality. Although their strategies can range across a continuum of personalities, game theorists have outlined a game with two main strategies: the HAWKs (bad aggressive individuals) and the DOVEs (the good individuals). Hawks always fight to kill or injure their opponents, whereas the doves display but never engage in serious fights. Shouldn't the doves become extinct in the population?

Can there be a middle path, between the dove and the hawk strategy?

No. Clearly an all-dove population is not stable since it can be easily invaded by a hawk. However, an all-hawk population is also not possible since these individuals will injure/kill each other (i.e., high cost) and not be able to produce offspring and propagate their genes. Hence, in such a population, being a dove can be useful and dove genes will spread in this population. In any conflict situation, although dove will always end up losing the resource to a hawk, but it never gets hurt (hence it never decreases in fitness) when confronting a hawk. Therefore the interactions are always neutral with respect to the dove's fitness. Personality research in invertebrates and vertebrates shows that although in the short term, aggressive individuals have an advantage (greater access to food and mates), they make bad parents and mates and hence have lower fitness overall [4]. Thus natural selection favours a mixed population of hawks and doves [2], where they have similar average payoffs and the two strategies are at equilibrium, hence are in an evolutionary stable state.

Can there be a middle path between the dove and hawk strategy?

Figure 3. A female chacma baboon with its young.
Photo: Shomen Mukherjee

What if individuals could assess the different roles within a strategy, and had the choice of playing each role when they thought it was appropriate? This means that although the frequency of hawk and dove strategy remains the same, the individual chooses when to play which strategy. Since now individuals have a choice of using a given strategy based on their assessment, it is now a hawk-dove ESS, compared to a hawk-dove evolutionary stable state. Such a strategy is called *Bourgeois* or the *Retaliator*. Such individuals always play hawk if they are an owner and a dove if they are an intruder. Bourgeois strategy has been observed among some group living mammals such as lions and primates. For example, it has been found [5] that in a hierarchical society such as that of baboons (*Figure* 3), if a particular male baboon had a bonding with a female, then a second male which has watched this relationship will not challenge the first male for ownership (i.e., male # 2 plays dove). If at a later time, the second baboon forms a relationship with another female, the first male will not challenge it (male # 1 now plays dove). This reduces the probability of injury for all males.

The Rock-Paper-Scissors Game: Nash Equilibrium that is not an ESS

One of the fascinating examples of a rock-paper-scissors game in Nature is the mating game between males of the side-blotched lizard (*Uta stansburiana*), [6]. These lizards are found in the coastal ranges of California, USA. In these lizards, males have three color morphs (strategy):

Evolutionary game theory had its origin in Charles Darwin's theory of Natural Selection.

• Orange throat – large and very aggressive and defend larger territories (territory includes animal foraging ground and mates).
• Blue throat – less aggressive, monogamous and have small territories.
• Yellow throat – sneaky and do not defend territories.

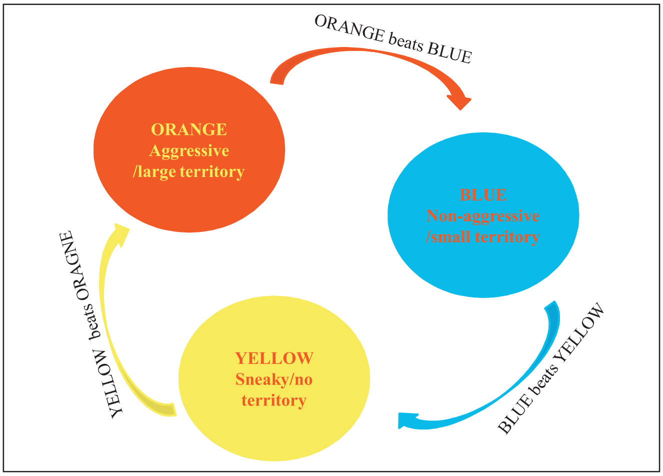

Figure 4. The perpetual game of rock-paper-scissor seen in the side-blotched lizards in coastal California.

In this game (*Figure* 4), 'orange' beats 'blue', as it is more aggressive and manages to mate with many more females, 'blue' beats 'yellow' as 'yellow' cannot fool him as he has only one female to protect, and 'yellow' beats 'orange', by sneaking up on his females and mating with them without having to guard any territory.

These three morphs have been locked in this perpetual game. When one color morph become more abundant in a population, females have the unique tendency to prefer the morphs that are rarer. The ratio of the three male morphs orbit around equilibrium (1/3, 1/3, 1/3), but it does not reach an ESS, however, the population reaches an evolutionary stable state.

Although humans compared to other species, are more intelligent and rational, *ESS* provided an elegant way of extending game theory to the 'less -gifted' members of the animal kingdom who might not make a conscious choice of a given strategy, but are rather genetically programmed to do so.

Nash Equilibrium and Evolutionary Game Theory: A Brief History

One of the most significant contributions of John Nash was in the field of *non-cooperative game theory* (part of classical game theory), which seeks to explain both cooperation and non-cooperation. He suggested a game where one looks at a combination of strategies, one per player. If the players act according to this combination, each player achieves his maximum payoff against any of the other strategies played by the other player. This is the Nash equilibrium point among the different strategies in a rational game [7], (described in detail elsewhere in this issue). In Nash equilibrium, no alternative strategies provide a better reply than the equilibrium, making the equilibrium point the best response of one player with regard to the other. Nash equilibrium point soon became revolutionary with its applications in the field of economics.

Although evolutionary game theory had its origin in Charles Darwin's[1] theory of natural selection[2], which states that the fittest genetic make up or the best behaviour or strategy is more likely to survive, be successful, and hence replicate (*survival of the fittest*) to the next generation [8]. In 1973, John Maynard Smith[3], a British theoretical evolutionary biologist, and George Price, a population geneticist, came up with a seminal concept 'ESS' [1], which changed the way biologists looked at things. The idea of ESS first evolved in the context of intra-specific (within species) outcomes, such as sex ratios and animal conflicts. Maynard-Smith and Price derived the theory of evolutionary games, partly from the theory of classical games and in part from the work of Robert MacArthur [9] and William Hamilton[10] on the evolution of sex ratios in animals. Julian Sorell Huxley had proposed [11] that ritualistic or *conventional* behavior (as *'C'* in ABOL–TABOL game) is more common, while the use of *dangerous* behavior or weapons (as *'D'* in ABOL–TABOL game) within a population is rare, as it would be selected against the survival of a species. Natural selection would select against individuals using a dangerous strategy. Individuals with such a strategy would become rare in the population simply because they would die of their injury. Later, Hamilton also proposed that excessively aggressive individuals will injure their close relatives and hence will be selected against in a population.

[1] See Renee M Borges, Revolutions in Evolutionary Thought: Darwin and After, *Resonance*, Vol.14, No.2, pp.102–123, 2009.

[2] See Sahotra Sarkar, Wallace and Natural Selection, 1858, *Resonance*, Vol.13, No.3, pp.236–244, 2008.

[3] See Vidyanand Nanjundiah, John Maynard Smith (1920–2004) – One of the last Grand Evolutionary Theorists of the 20th Century, *Resonance*, Vol. 10, No.11, pp.70–78, 2005.

After Maynard-Smith and Price [1] mathematically derived why a given behaviour or strategy was adopted by a certain proportion of the population at a given time, it was shown that a strategy which is currently stable in a population need not be stable in evolutionary time (across generations). Additionally it was suggested that an individual may play a mixture of strategies. In 1981 Robert Axelrod conducted a computer tournament where people were invited to submit strategies for playing 200 prisoner's dilemma game [12], and the strategy which won was the simple Tit-for-Tat strategy, submitted by Anatol Rapoport. This strategy had two rules, on first move cooperate, and on the successive moves do what your opponent did in the previous move. Tit-for-Tat proved to be an ESS strategy, a very important strategy which could help explain reciprocal altruistic behaviour among animals.

Evolutionary games are not only prevalent in large mammals like cats, deer, mice, and monkeys, but this type of games are seen in smaller invertebrates such as *Daphnia*, dung beetles, microbes and also in plants.

Though derived from the classical game theory, evolutionary game theory is different from the classical game theory in its assumptions [13].

1. *Rationality vs. natural selection*: In a classic rational game, all players know the full structure of the game and make conscious and rational choices to play the game. Here, the assumption is that all humans are rational and an agent or player in a game thinks or reasons rationally and intelligently and plays each move strategically. Although humans compared to other species, are more intelligent and rational, ESS [1] provided an elegant way of extending game theory to the 'less-gifted' members of the animal kingdom who might not make a conscious choice of a given strategy, but are rather genetically programmed to do so. Initially, ESS was described as a systematic equilibrium in a two-person (or two-strategy) game, in which the winner is the individual who continues for longer. An individual who can play longer will generally be larger and healthier and hence, natural selection will favor those traits. However, larger body size might be a disadvantage while running from predators. Additionally, the size and strength of an animal may not change day-to-day, but can change with age, which might impact the frequency of these traits (and underlying genes) in a population [14]. Considering that the different players in a game are members in a population of a species, the population can be divided into 'n' number of strategies. Evolutionary games will consider the circumstances under which the frequency of one strategy is stable against the frequency of others in a population. Therefore, real life games, where outcome of a strategy depends on the *physical* environment

(where the player is) and the *social* environment (with whom the player is interacting), situations become more complicated.

2. *Payoff vs. fitness*: In the classical game theory (e.g., Nash's equilibrium theory), the winning or losing of a strategy is the payoff of a particular strategy (utility function) (*Figure* 2). In evolutionary games, this pay-off or the utility function is an equivalent of the fitness function. Since natural selection is ruled by the survival of the fittest, the fitness of an individual is the number of offspring an individual can conduce to the next generation. In other words, this is the model of replication of a strategy (DNA replication) so that it is carried over to the next generation.

Similar to the classical games, the evolutionary games also follow certain assumptions [2], such as:

[4] In biology, a mutant is an organism with a new genetic character, often a result of mutation (a permanent alteration of nucleotide sequence in the genome). If such an individual has a new strategy, it would be called a mutant strategy.

a) In a mixed-strategy population, the sum of frequencies of the strategies will be equal to 1.
b) Depending on the mutant strategy[4], which is against the parent strategy, a mutant will either infiltrate or die-off in a population.
c) Member of a population will be paired randomly.
d) Birth and death rates are constant.

Evolutionary games are not only prevalent in large mammals like cats, deer, mice, and monkeys, but this type of games are seen in smaller invertebrates such as *Daphnia* (water flea), dung beetles, microbes and also in plants. For example, its has been shown [15] that in plants, investment in plant height improves their access to light, but imposes costs in construction and maintaining a large trunk that defies gravity. However, for a single plant, its access to light will depend on other height-strategies that are present in the neighborhood. Falster and Westoby [15] identified 14 ESS of traits that influence this competition for light. There is a diversity of such examples in Nature. The very fact that different strategies are coexisting in Nature tells us about a successful ESS. ESS was introduced to address the prevalence of ritual fighting in interspecific animal conflicts, which ultimately led to explorations in asymmetric and multistep games. From conflicts of mate choice, sibling rivalry, parent–offspring antagonism to theories of social foraging, dispersal, habitat selection, as well as evolutionary arms race between predator and prey and virus and host, ESS has been widely applied in biology [16].

Although Nash's equilibrium point became widely accepted in the context of rational games, in his unpublished PhD dissertation, John Nash had provided another interpretation of his equilibrium, the population-statistics [7]. As opposed to the rational interpretation, where the game is played only once, in this approach the game is played over and over again and the players do not actually know the structure of the game. In his thesis Nash stated:

> *It is unnecessary to assume that the participants have full knowledge of the total structure of the game, or the ability and inclination to go through any complex reasoning processes. But the participants are supposed to accumulate empirical information on the relative advantages of the various pure strategies at their disposal. Since there is to be no collaboration between individuals playing in different positions of the game, the probability that a particular n-tuple of pure strategies will be employed in a playing of the game should be the product of the probabilities indicating the chance of each of the n pure strategies to be employed in a random playing.*

The concept of dynamic stability aims to understand what happens when the population state is slightly perturbed, particularly when invaded by a rare (once extinct) strategy.Although not widely known, Nash did identify dynamically stable population states in large strategically interacting populations [17]. This suggests that although biologists were unaware of this contribution of Nash to ESS, his ingenuity was undoubted. He indeed had a 'beautiful mind'.

Acknowledgements

We would like to thank the Chief Editor, Prof. Rajaram Nityananda, for inviting us to write this article and for his valuable comments.

Also thanks to Ayan Guha for making the cat sketches at such a short notice.

Suggested Reading

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