An Evolutionary Stable Strategy is a set of behaviours, which, if followed by the whole population, cannot be invaded by any mutant strategy that is initially sparse among the population. J. Maynard Smith explains the importance of this definition as follows:

> *"In a population consisting entirely of individuals adopting strategy **I**, rare variants arising by mutation which adopted a different strategy **J** would not increase in frequency, and hence the population would be stable under mutation and selection."* [1]

Once an ESS becomes fixed, any new alternative strategy cannot take over by natural selection alone. This does not take into account external changes, or changes to the environment.

A commonly analysed example within the field of game theory is the game called "Prisoner's Dilemma". This is used to show how two perfectly rational individuals may choose not to co-operate, despite it appearing in their best interest to do so. Formalised in 1992, the game presents two individuals a choice; either remain silent or betray the other. Should both remain silent, the sentence would be 1 year. If one of them betrays but the other remains silent, the defector is set free and the betrayed is sentenced to 3 years. However, if both defect, the sentence becomes 2 years for both. The assumptions being made are that the prisoners cannot communicate, and both are familiar with the game.

In this scenario, while both remaining silent would be the globally optimal choice, it is not optimal when viewed from an individual perspective. From the standpoint of prisoner A, B can either defect or remain silent. In the first case, it is better for A to defect, since a sentence of 2 years is preferable to 3. Should B remain silent, it is still better for A to defect, since being set free is better than spending 1 year in prison. Since the game is symmetric, B's decision will be similar. A stable state is reached, in which both players defect, resulting in a globally worse situation.

If the game is played multiple times with the players remembering the previous actions, a multitude of strategies can arise. Among these are "Always Co-operate", "Always Defect", "Blow-for-Blow". Studies of the Iterated Prisoner's Dilemma show that greedy strategies tend to fare worse than co-operative behaviour. This led to a possible explanation for the evolution by natural selection of altruistic behaviour. The best strategy to emerge, "Blow-for-Blow" strategy involves co-operating the first turn, then copying the opponent's previous move.

Animal behaviour can be simplified to a game of Prisoner's Dilemma. An example of this is presented in Richard Dawkins's book, *"The Selfish Gene"*, where vampire bats engage in food sharing. [3]

Prisoner's Dilemma can also be used to explain arms races. Even though costly, arming itself presents a country with a strategic advantage, should the opponent choose not to.

[1] J. Maynard Smith, “The Theory of Games and the Evolution of Animal Conflicts”, 1974 http://physwww.mcmaster.ca/~higgsp/756/WarOfAttrition.pdf

[2] Robert Axelrod, “The Evolution of Cooperation”, 1984
https://www-ee.stanford.edu/~hellman/Breakthrough/book/pdfs/axelrod.pdf

[3] Richard Dawkins, “The Selfish Gene”, 1976
http://www.arvindguptatoys.com/arvindgupta/selfishgene-dowkins.pdf

[4] Stephen J. Majeski, "Arms races as iterated prisoner's dilemma games", 1984