Evolutionarily Stable Strategies

E Pianka

doi: 10.1006/rwgn.2001.0431

Pianka, E
Section of Integrative Biology, University of Texas at Austin, Austin, Texas 78 712-1064, USA

When natural selection acts on several different alternative behaviors, the most optimal should be favored. If costs and benefits of alternatives depend on choices made by other individuals, optimal solutions are not always as obvious as they are in simpler situations. An evolutionarily stable strategy, or ESS, is a mathematical definition for an optimal choice of strategy under such conditions.

Interactions between two individuals can be depicted as a mathematical game between two players. A branch of mathematics, called game theory, seeks to find the best strategy to play in any given carefully defined game. The central problem of game theory is to find the best strategy to take in a game that depends on what other players are expected to do.

Originally used in studies of economics and human conflicts of interest, game theoretical thinking was first used in biology by Hamilton, 1967 to study evolution of sex ratios. Later, game theory was explicitly applied to behavioral biology by Maynard Smith, 1972 and Maynard Smith and Price, 1973. Maynard Smith coined the term ESS for a refinement of the Nash equilibrium used by economists to define a solution to a game.

The notion of a Nash equilibrium makes some tacit assumptions about rational foresight on the part of the player. An ESS must meet a stricter set of requirements than Nash equilibria, the mathematical difference boils down to whether a tie between strategies leads to a new strategy being considered better. An ESS attempts to define conditions under which blind evolution will return to the strategy in question, rather than requiring rational foresight to dissuade the exploration of alternatives.

An ESS is a strategy that cannot be beaten by any other strategy. An individual adopting it outperforms any individual adopting any alternative tactic. No other strategy can outperform an ESS. Individuals adopting an ESS tactic have a higher reproductive success than individuals adopting other tactics. Such an unbeatable tactic can go to fixation (100%) in a population and such a population cannot be invaded by any other tactic. Inevitably, an ESS ends up encountering itself more often than it confronts any other strategy, and it must therefore perform better against itself than any other strategy can perform against it.

Game theory involves conflicts of interest in which the value of a given action by a decision maker depends both on its own choices as well as on those of others. A 'payoff' matrix of values of outcomes is postulated based on the respective behaviors of two or more contestants under all possible situations. Payoffs are frequency dependent. Decision rules that represent an evolutionarily stable solution to such an evolutionary game constitute an ESS (Axelrod and Hamilton, 1981.

As an example, consider a well known game theoretical model called the "prisoner's dilemma." In this hypothetical situation, two partners in crime have been arrested. The police interrogate each person alone. Each party could cooperate with the other and steadfastly refuse to squeal on their friend. If both cooperate and remain silent, the authorities cannot establish guilt and both get off scott free (loyalty pays off). Alternatively, each could betray their partner and confess. Now consider respective rewards and punishments received by each partner for making each decision. If only one party confesses while the other remains quiet, this betrayal is rewarded by giving the confessor a light sentence for providing "state's evidence" and testifying as to the guilt of their loyal silent partner, who is then found guilty and receives a much longer prison term (they getthe "sucker's pay off").
However, if both partners tell, the authorities put both on trial and both receive moderate, but not long, sentences of imprisonment. In a 'zero sum' game, all losses add up to equal all gains. Not so in this game, where each partner can gain considerably without as much loss to the other (indeed, by working together, both could escape conviction altogether). But they are not allowed to work together and neither knows what the other will do.

Here then, is the classic "prisoner's dilemma": each prisoner must decide what to do without knowing what decision the other will make. What is the best strategy? Confess to the crime! Any attempt to cooperate could lead to the 'sucker's pay off,' but confession results either in a light sentence or a moderate one. Avoid the worst situation. In such a symmetric nonzero sum game, both partners betray the other's confidence and both do moderate 'time.' Although both partners would have been better off if they had cooperated, the best solution for each person individually in isolation is to defect rather than take the risk of being loyal but being betrayed and ending up with the inglorious 'sucker's pay off.'

The "prisoner's dilemma" game involves just one decision. Suppose instead, that participants interact repeatedly and that each knows that the other will be encountered again and again. Now many decisions must be made in sequence. In such a situation, "the future can cast a long shadow backwards onto the present" (Axelrod, 1984). Cooperation can evolve under such a long-term situation. Consider the evolutionary game "tit for tat," the rules of which are cooperate on the first encounter but then copy the behavior of the other player on all subsequent encounters. Using this strategy, a player always cooperates on its first encounter. But, if player B defects, player A retaliates on its next move. In a population composed of a mixture of players with a variety of behavioral strategies, an individual employing the tit for tat strategy does well. When interacting with cooperative individuals, players always cooperate to the mutual advantage of both. If the other player does not cooperate, the two may then retaliate all the time, and the tit for tat player will receive none of the advantages of cooperation. The initial attempt at cooperation will incur only a minor cost. The tit for tat strategy is most profitable, quickly spreading to fixation. When the entire population employs the tit for tat strategy, it cannot be invaded by individuals employing most other tactics – tit for tat is normally an ESS (but see below for an exception).

Axelrod, 1984 identified three behavioral tendencies that would favor the evolution of cooperation: (1) being 'nice' (never first to defect); (2) being 'provocable' (retaliate against defection); and (3) being 'forgiving.' The first two are the hallmarks of tit for tat. The third, allowing bygones to be bygones and resuming cooperation is the strategy known as 'generous tit for tat,' unusual in that it can invade tit for tat under certain conditions. Possession of these three behavioral traits make it more likely that both parties will reap the benefits of mutual cooperation. Many highly social animals do indeed display these three behaviors.

The above examples illustrate 'pure' strategies: always adopt a single, best rule of behavior. Such an outcome often arises in contests with just two contestants. However, when an individual must play against an entire population of other individuals, ESS solutions are often 'mixed,' with probabilistic rules determining the chosen strategy. In a particular situation, be a bully with probability p but be cowardly with probability q. At equilibrium, a fraction p of the population will be bullies and another fraction q will be cowards, with each tactic doing equally well overall. Overall benefit to all bullies equals overall benefit for all cowards. If the proportions in the population deviate toward too many bullies, cowards outperform bullies, whereas if there are too many cowards, bullies perform better. This is the classic hawk–dove game. Sex ratios are similar: if males are in short supply, on average an individual male will contribute more genes to the next generation than an individual female (and vice versa if females are scarce). These are also examples of frequency-dependent selection.

ESS rules can also be 'conditional,' taking a form like "if hungry, be a bully, but if satiated be a coward" (Enquist, 1985). In the real world, most behaviors are probably closely attuned to such immediate environmental situations. Often, combatants are not equal, leading to conditional rules, such as "fight if I'm bigger" but "flee if I'm smaller" (Hammerstein, 1981). Such rules lead to pecking orders with larger animals dominant over smaller ones. Because even the winner can be injured in a fight, fights are best avoided by both contestants if the outcome is already relatively certain. Often, ritualized appeasement behaviors and postures are adopted by the loser, effectively curtailing aggressive behaviors of winners. Indeed, fights only make evolutionary sense when two contestants are closely matched and each is equally likely to win (Enquist and Leimar, 1983). In such a situation, fights escalate and serious injuries can occur. Often the loser gives up abruptly and flees, but holds its stance almost as a bluff, right up until the end. Among many animals, residents typically win in encounters with vagrants – the first animal to arrive seems to acquire ownership and the motivation to defend its turf. Game theory easily accommodates such flexible behavior (Maynard Smith and Price, 1976). The ESS approach has been particularly useful in analyzing the evolution of communication (Johnstone, 1997).

References

Axelrod R and Hamilton WD (1981) The evolution of cooperation. *Science* 211: 1390–1396.

Axelrod R (1984). *The Evolution of Cooperation*. New York: Basic Books.

Enquist M (1985) Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behavior* 33: 1152–1161.

Hamilton WD (1967) Extraordinary sex ratios. *Science* 156: 477–488.

Hammerstein P (1981) The role of asymmetries in animal contests. *Animal Behaviour* 29: 193–205.

Johnstone RA (1997) The evolution of animal signals. In: *Behavioural Ecology: An Evolutionary Approach*, 4th edn, pp. 155–178. Blackwell Scientific.

Maynard Smith J (1972) *On Evolution*. Edinburgh: Edinburgh University Press.

Maynard Smith J (1982) *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Maynard Smith J and Price GR (1973) The logic of animal conflict. *Nature* 246: 15–18.

Maynard Smith J and PG(1976) The logic of asymmetric contests. *Animal Behaviour* 24: 159–175.

Maynard Smith J and Parker, GA (1976) The logic of asymmetric contests. Animal Behaviour 24: 159-175.

***See also:* 0581, 0430**