Game Theory Principles VIII

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Game theory in biology: Evolutionary game theory. Evolutionary stability, evolution of sex ratios, the peacock's tail, costly signaling. Concepts: Maximization of reproductive success, Evolutionarily Stable Strategy (ESS).

Some biological phenomena to which game theory has been applied:

1. The evolution of sex ratios.
2. Why do peacocks have such long tails?
3. The evolution of root systems.
4. The evolution of display behavior.

1. In humans the sex ratio at birth is approximately 105:100, slightly favoring males.
2. Why is the human sex ratio not exactly equal to one?
3. Why is the sex ratio different in other species?
4. Why are sex ratios in other species frequently extreme?

In 1710 John Arbuthnot empirically investigated the sex ratio and found an approximate 1:1 ratio. He concludes:

For hence it follows that Polygamy is contrary to the Law of Nature and Justice, and to the Propagation of Human Race; for where Males and Females are in equal number, if one Man takes Twenty Wives, Nineteen Men must live in Celibacy, which is repugnant to the Design of Nature; nor is it probable that Twenty Women will be so well impregnated by one Man as by Twenty. (cited in Brian Skyrms, *Evolution of the Social Contract*)

In essence Arbuthnot ‘derives’ the 1:1 sex ratio from monogamy (which leaves open the question of why frequently this ratio is 1:1 among mammals that are not monogamous).

Darwin found the sex ratio problem vexing. He stated in 1871:

In no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; for instance, an individual with a tendency to produce more males than females would not succeed better in the battle for life than an individual with an opposite tendency;

and therefore a tendency of this kind could not be gained through natural selection ... I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution to the future.(cited in Brian Skyrms, *Evolution of the Social Contract*)

In 1930 Ronald A. Fisher outlined an explanation for the 1:1 sex ratio in his book *The Genetical Theory of Natural Selection.*

According to Fisher the sex ratio is genetically determined. If there is an excess of males (females) in the population it becomes advantageous to have more female (male) offspring. This favors a genetic disposition for a lower (higher) sex ratio. In equilibrium the sex ratio is 1:1.

In 1967 William D. Hamilton addressed the problem of **extraordinary sex ratios** from an evolutionary perspective.

Hamilton introduced the concept of an **unbeatable strategy** which foreshadowed John Maynard Smith and George R. Price's

evolutionarily stable strategy (ESS).

In evolutionary game theory Darwinian fitness (reproductive success) takes the role of payoffs (utility) in conventional game theory.

An organism's **phenotype** is any observable trait or behavior of an organism.

A strategy in evolutionary game theory is a behavioral phenotype.

John Maynard Smith defines an evolutionarily stable strategy as *"... a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection."* John Maynard Smith in *Evolution and the Theory of Games.*

The Hawk-Dove Game

1. Two animals are contesting a resource with value V (such as a favorable habitat, food or mates).
2. V can be thought of as the increment in **Darwinian fitness** that is derived from acquiring the resource.
3. Suppose that each animal can adopt two strategies, **Hawk** and **Dove**, one aggressive, the other accommodating.

A more detailed description of the strategies:

1. **Hawk:** Escalate and continue until injured or until the opponent retreats.
2. **Dove:** Display and retreat immediately if the opponent escalates.

Payoffs in the Hawk-Dove Game:

1. If a Dove strategy encounters a Hawk strategy, the Dove retreats and has a payoff (increase in Darwinian fitness) of 0.
2. If a Dove meets a Dove, they split the resource and each have a payoff of $V/2$.
3. If Hawk meets a Hawk they fight until one is injured and forced to retreat. The cost of injury equals C and the resulting payoff is $\frac{V-C}{2}$.
4. If a Hawk meets a Dove, he captures the resource for a payoff of V.

Payoffs in the Hawk-Dove Game

	Hawk	Dove
Hawk	$\frac{V-C}{2}$	V
Dove	0	$\frac{V}{2}$

Game VIII-1

1. Let there be a large population (infinite).
2. Each individual in the population adopts either the Hawk strategy, H, or the Dove strategy, D.
3. Individuals are randomly paired.
4. Each individual's initial fitness equals W_0.

Define:

1. $p :=$ the frequency of H in the population, or the probability with which a common mixed strategy in the population chooses H.
2. $W(H) :=$ fitness of H
3. $W(D) :=$ fitness of D
4. $E(H, D) :=$ payoff of H against D, etc.

Then each strategy's fitness in a population with a proportion p of Hawks equals:

$$\begin{aligned} W(H) &= W_0 + pE(H,H) + (1-p)E(H,D) \\ W(D) &= W_0 + pE(D,H) + (1-p)E(D,D) \end{aligned}$$

A strategy I is stable if when nearly all individuals adopt it, then these individuals have greater fitness than any possible mutant.

Let $pI + (1-p)J$ indicate a population in which a proportion p adopt strategy I and a proportion $(1-p)$ adopt strategy J.

Define:

$$
\begin{aligned}
W(I, pI + (1-p)J) &:= I\text{'s fitness in a population with a} \\
&\quad\ \text{proportion } p \text{ of } I \text{ strategies} \\
W(J, pI + (1-p)J) &:= J\text{'s fitness in a population with a} \\
&\quad\ \text{proportion } p \text{ of } I \text{ strategies}
\end{aligned}
$$

With pairwise contests, as in the Hawk-Dove game, and random matching, we have

$$
\begin{aligned}
W(I, pI + (1-p)J) &= W_0 + pE(I, I) + (1-p)E(I, J) \\
W(J, pI + (1-p)J) &= W_0 + pE(J, I) + (1-p)E(J, J)
\end{aligned}
$$

The (mixed) strategy I is evolutionarily stable if for any mutant strategy J and sufficiently small $1-p$:

$$W(I, pI + (1-p)J) > W(J, pI + (1-p)J)$$

With pairwise contests and random matching, this condition is equivalent to:

The mixed strategy I is an **evolutionarily stable strategy (ESS)** if for all strategies $J \neq I$ we have:

1. $E(I, I) > E(J, I)$, or
2. $E(I, I) = E(J, I)$, and $E(I, J) > E(J, J)$.

Notice that an ESS is a symmetric Nash equilibrium with an **additional stability condition.**

The ESS definition implicitly refers to an environment

1. with a **large population**,
2. with **random interactions** among members of the population,
3. with a **monomorphic** population (in equilibrium each member of the population adopts the same behavior),
4. with **asexual reproduction**,
5. where **mixing is heritable** behavior,
6. where behaviors **breed true**,
7. where individuals only engage in **pairwise contests**, and
8. where there are only **symmetric contests**.

In the Hawk-Dove game

1. Dove is not an ESS, and
2. Hawk is an ESS if $V - C > 0$.
3. What if $V - C < 0$?

If $V < C$ in the Hawk-Dove game, our only hope for an ESS is a mixed Nash equilibrium.

In a mixed equilibrium, I , the payoffs from the two pure strategies, H and D, in the support of the equilibrium strategy must be the same:

$$E(H, I) = E(D, I).$$

If the equilibrium strategy I assigns probability p to H and probability $1-p$ to D, this indifference condition can be restated as

$$pE(H,H)+(1-p)E(H,D) = pE(D,H)+(1-p)E(D,D),$$

or

$$p\frac{V-C}{2}+(1-p)V = p0+(1-p)\frac{V}{2},$$

or

$$p = \frac{V}{C}.$$

Let's check whether the mixed strategy I with mixing probability $p = \frac{V}{C}$ is an ESS.

Since I is a mixed-strategy equilibrium, we have $E(I, I) = E(D, I) = E(H, I)$. Therefore, we need to check the second condition in the definition of an ESS:

$$E(I, D) = pV + \frac{1}{2}(1-p)V > \frac{V}{2} = E(D, D)$$
$$E(I, H) = \frac{1}{2}p(V - C) = pE(H, H) > E(H, H),$$

where we use the facts that $p \in (0, 1)$ and $V < C$.

“Playing the Field”

Frequently, competition does not occur in pairwise contests; e.g.

1. plants compete with all their neighbors, and
2. the fitness of a genetically transmitted sex ratio depends on a characteristic of the entire population.

It is common to refer to such contests as “playing the field” contests.

The appropriate evolutionary stability condition for playing the field contests remains:

The strategy I is evolutionarily stable if for any mutant strategy J and sufficiently small $1-p$:

$$W(I, pI + (1-p)J) > W(J, pI + (1-p)J)$$

It is important to note, however, that unlike with pairwise random matching, the fitness function $W(I, pI + (1-p)J)$ need no longer be linear in the probabilities; i.e., in general

$$W(I, pI + (1-p)J) \neq pW(I, I) + (1-p)W(I, J).$$

An example of a playing-the-field model is the **Sex ratio game.**
Assume

1. Each female can produce N offspring.
2. The proportion of male offspring, s, is a heritable trait.
3. One male suffices to fertilize all females in the population.
4. All female eggs are fertilized.

Fitness can be measured as the expected number of grandchildren.

Then, in a random-mating population with sex ratio s', the fitness of the strategy s equals:

$$W(s, s') = N^2 \left[1 - s + s \frac{1 - s'}{s'} \right].$$

To understand this expression, note that the number of female offspring is $(1 - s)N$, each of whom will have N children, for a total of $N^2(1-s)$ grandchildren from daughters.

The number of male offspring is $s \cdot N$; in a randomly mating population, the number of females fertilized by a son equals the number of females divided by the number of males (i.e. $\frac{1-s'}{s'}$). Hence, the number of grandchildren from sons equals $N^2 s \frac{1-s'}{s'}$.

Suppose that there are two possible heritable sex ratios in the population:

1. $s_1 = 0.1$, and
2. $s_2 = 0.6$

Then we can construct the following fitness matrix for the sex ratio game

		Population	
		$s'_1 = 0.1$	$s'_2 = 0.6$
Mutant	$s_1 = 0.1$	1.8	0.967
	$s_2 = 0.6$	5.8	0.8

Game VIII-2

The payoff matrix shows that neither the strategy s_1 nor the strategy s_2 is an ESS.

If only the two types of strategies s_1 and s_2 are possible, an ESS $\hat{s}$ satisfies:

$$W(s_1, \hat{s}) = W(s_2, \hat{s}),$$

i.e.

$$1 - 0.1 + 0.1\frac{1-\hat{s}}{\hat{s}} = 1 - 0.6 + 0.6\frac{1-\hat{s}}{\hat{s}},$$

which implies

$$\hat{s} = 0.5,$$

which requires 20% s_1 strategies and 80% s_2 strategies in the population (note that this is a stable polymorphism).

You might want to verify that this conclusion does not crucially depend on the choice of the two ratios s_1 and s_2.