

Discussion I Handout

April 2nd & 7th

Evolutionarily Stable Strategies

Overview

In the lecture on March 27th, we studied the application of game theory to the game of survival that genes, organisms, and even societies play. It was shown that in the short term, a completely selfish strategy is optimal in terms of payoff or benefit to the individual, but that when considered over longer time scales, when the game is played many times, then altruistic strategies are optimal. Which strategy is best depends on the context, including the rules of the game (including how many times the game will be played, and whether the players know how many times the game will be played) and, especially, what other strategies, any in what proportions, are in the population of game players. In this discussion we will explore this latter idea in more detail than was possible in the lecture.

Evolutionarily Stable Strategies

An important consideration with any approach to solving a problem is: “How robust is your approach?” Ideally, your approach to solving a problem, or your strategy for player a game should be a good general approach which works well under a variety of conditions. Think of it in terms of design: if the design of your car is robust, then it not only performs well when you are driving along the road in a straight line in good weather at a moderate speed by yourself, but also performs well when you are taking a corner a little faster than you should, when it is raining, when you are braking to avoid other cars, and so on. A strategy for playing the survival game for organisms is robust if it works well when the ecosystem changes or when other organisms change their own strategies for survival.

In the Prisoner’s Dilemma game, a strategy is robust if it performs well in a variety of populations, and in particular, if it does well when most members of the population adopt it. After all, in an evolutionary context, if a strategy is a good one, then more and more organisms will evolve to use that strategy, and so the natural result will be for the whole population to move towards that strategy; if the strategy is to be maintained over a long time, then it must be such that individuals continue to do well when most of the population adopt it, and there will not, for example, be wide swings back and forth between various strategy in the population as a whole.

An Evolutionarily Stable Strategy (ESS) is defined as “a strategy which, if most members of a population adopt it, can not be bettered by an alternate strategy” (Richard Dawkins, *The Selfish Gene*, p.69). An ESS is one which plays well with others of its kind, and also does well against invaders who try to take over the population. Once it takes over most members of a population, it tends to remain “in power” and be stable under some amount of variation in the population, and even perhaps in the strength of

rewards and punishments. If the dominant strategy is not an ESS, it will soon “topple” when mutants arise or arrive in the population, which will take over.

Thus ESSs are extremely important, because in a realistic setting, they are the only strategies which can be maintained over long periods of time. In this discussion activity we will investigate whether some of our basic strategies are ESSs or not.

Sample Strategies

Recall from the lecture the following matrix of payoffs and some sample strategies:

	Cooperate	Defect
Cooperate	\$300	-\$100
Defect	\$500	-\$10

- Angel = Always cooperate
- Devil = Always defect
- Tit-for-Tat (TFT) = Cooperate on first move; thereafter copy your opponent's last move

Experiments

We will consider a number of examples of populations consisting of some combinations of the above four basic strategies, and try to investigate how well these strategies do against each other, and whether they are ESSs. In each case, assume that each iterative game is played many times, so that the reward or punishment in the first round is not always significant. For example, if TFT plays a Devil, then over time, the payoff gets closer and closer:

Round	T's Move	D's Move	T's Score	D's Score	T's Total	D's Total	T's Avg/Rnd	D's Avg/Rnd
1	C	D	-\$100	\$500	-\$100	\$500	-\$100.00	\$500.00
2	D	D	-\$10	-\$10	-\$110	\$490	-\$55.00	\$245.00
3	D	D	-\$10	-\$10	-\$120	\$480	-\$40.00	\$160.00
4	D	D	-\$10	-\$10	-\$130	\$470	-\$32.50	\$117.50
5	D	D	-\$10	-\$10	-\$140	\$460	-\$28.00	\$92.00
6	D	D	-\$10	-\$10	-\$150	\$450	-\$25.00	\$75.00
7	D	D	-\$10	-\$10	-\$160	\$440	-\$22.86	\$62.86
8	D	D	-\$10	-\$10	-\$170	\$430	-\$21.25	\$53.75
9	D	D	-\$10	-\$10	-\$180	\$420	-\$20.00	\$46.67
10	D	D	-\$10	-\$10	-\$190	\$410	-\$19.00	\$41.00
100	D	D	-\$10	-\$10	-\$1,090	-\$490	-\$10.90	-\$4.90
200	D	D	-\$10	-\$10	-\$2,090	-\$1,490	-\$10.45	-\$7.45
500	D	D	-\$10	-\$10	-\$5,090	-\$4,490	-\$10.18	-\$8.98
1000	D	D	-\$10	-\$10	-\$10,090	-\$9,490	-\$10.09	-\$9.49

For this reason, it is usual (but not always) appropriate to just think about what happens over the long term. For example, it is apparent from the above chart that to a Devil, a TFT player just looks like another Devil (after an initial “misunderstanding”). Similarly, to an Angel, TFT looks like another Angel.

Experiment One

The Question: How well does each of these strategies do against each other?

What to do:

- a) Consider what happens when each of the three strategies plays against itself and against the other two. What is the average payoff per round for each of these? Fill in the following chart (for each cell fill in the bottom left with the score of the strategy on the left, and the upper right with the score of the strategy on top):

	Devil	Angel	TFT
Devil			
Angel			
TFT			

Experiment Two

Investigation: Is Angel an ESS?

Questions to ask:

- a) Suppose you have a very large population of Angels, and a mutant TFT develops (or an TFT arrives from outside and becomes part of the community). What happens? Who would be aware that the newcomer is an TFT and not an Angel?
- b) Now suppose a single Devil arrives in a population of Angels? What happens?

- c) Suppose that high scores are represented not by money, but by reproductive success (i.e. offspring); what do you suppose will happen to the population of Angels and one Devil over time?
- d) Is Angel an ESS?
- e) Same question as last one, but for the population of Angels with one TFT.

Experiment Three

Investigation: Is Devil an ESS?

Questions to ask:

- a) Suppose you have a very large population of Devils, and a mutant Angel develops (or arrives from outside and becomes part of the community). What happens?
- b) Now suppose a single TFT arrives in a population of Devils? What happens? In this case, do consider what the effect of the very first round is.
- c) Suppose that high scores are represented not by money, but by reproductive success (i.e. offspring); what do you suppose will happen to the population of Devils and one Angel over time?
- d) Same question as last one, but for the population of Devils with one TFT.
- e) Finally, suppose TWO TFTs arrive in a large population of Devils. Now what is the average score over many generations, and what would happen if the payoff were in terms of children rather than money?

Experiment Four

Investigation: Is TFT an ESS?

Questions to ask:

- a) Suppose you have a very large population of TFTs, and a mutant Devil develops/arrives. What would be the effect on payoffs and offspring, as considered above?
- b) Now suppose a single Angel arrives in a population of TFTs? What happens?

Experiment Five

Investigation: Under what conditions can TFT be invaded by alternate strategies?

What to do:

- a) Consider what would happen if a population of mixed TFTs and Angels has an invasion by a single Devil. Consider (i) a population mostly consisting of TFTs with some Angels, and (ii) a population consisting of mostly Angels and some TFT. Note that the previous experiments show that Angels and TFTs have no relative advantage, and that the survival advantage of each might depend on other factors not part of this particular game. Suppose the population varied over time with different percentages of TFT and Angels. When might a Devil gain a “toe-hold” and invade?
- b) We stated above that TFT was an ESS; however, does this mean that it can NEVER be invaded under any circumstances?

Experiment 2(a): Angels plus TFT invader

Experiment 2(b): Angels plus Devil invader

Experiment 3(a): Devils with Angel invader

Experiment 3(b): Devils with TFT invader

Experiment 3(e): Devils with two TFT invaders

Experiment 4(a): TFTs with Devil invader

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=====
Generation 1
=====
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
2790   Devil 1  1  1  1  1  1  1
=====

Generation 2
=====
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
5580   Devil 1  1  1  1  1  1  1
=====

Generation 3
=====
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
143130 TFT  2  1  2  2  1  2  1
8370   Devil 1  1  1  1  1  1  1
=====

Generation 4
=====
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
190840 TFT  2  1  2  2  1  2  1
11160   Devil 1  1  1  1  1  1  1
=====

Generation 5
=====
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
238550 TFT  2  1  2  2  1  2  1
13950   Devil 1  1  1  1  1  1  1
=====
```

Experiment 4(b): TFT with Angel invader

Experiment 5(a).1: 9 TFTs, 1 Angel; Devil invading

=====

Generation 1

=====

53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
53710	TFT	2	1	2	2	1	2	1
52000	Angel	2	2	2	2	2	2	2
12790	Devil	1	1	1	1	1	1	1

=====

Generation 2

=====

107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
107420	TFT	2	1	2	2	1	2	1
104000	Angel	2	2	2	2	2	2	2
25580	Devil	1	1	1	1	1	1	1

=====

Generation 3

=====

161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
161130	TFT	2	1	2	2	1	2	1
156000	Angel	2	2	2	2	2	2	2
38370	Devil	1	1	1	1	1	1	1

=====

Generation 4

=====

214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
214840	TFT	2	1	2	2	1	2	1
208000	Angel	2	2	2	2	2	2	2
51160	Devil	1	1	1	1	1	1	1

=====

Generation 5

=====

268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
268550	TFT	2	1	2	2	1	2	1
260000	Angel	2	2	2	2	2	2	2
63950	Devil	1	1	1	1	1	1	1

Experiment 5(a).2: 6 TFTs, 4 Angels; Devil invading

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=====
Generation 1
=====
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
47710  TFT  2  1  2  2  1  2  1
46000   Angel 2  2  2  2  2  2  2
46000   Angel 2  2  2  2  2  2  2
46000   Angel 2  2  2  2  2  2  2
46000   Angel 2  2  2  2  2  2  2
41550   Devil  1  1  1  1  1  1  1
=====

Generation 2
=====
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
95420  TFT  2  1  2  2  1  2  1
92000   Angel 2  2  2  2  2  2  2
92000   Angel 2  2  2  2  2  2  2
92000   Angel 2  2  2  2  2  2  2
92000   Angel 2  2  2  2  2  2  2
83100   Devil  1  1  1  1  1  1  1
=====

Generation 3
=====
143130  TFT  2  1  2  2  1  2  1
143130  TFT  2  1  2  2  1  2  1
143130  TFT  2  1  2  2  1  2  1
143130  TFT  2  1  2  2  1  2  1
143130  TFT  2  1  2  2  1  2  1
138000   Angel 2  2  2  2  2  2  2
138000   Angel 2  2  2  2  2  2  2
138000   Angel 2  2  2  2  2  2  2
138000   Angel 2  2  2  2  2  2  2
124650   Devil  1  1  1  1  1  1  1
=====

Generation 4
=====
190840  TFT  2  1  2  2  1  2  1
190840  TFT  2  1  2  2  1  2  1
190840  TFT  2  1  2  2  1  2  1
190840  TFT  2  1  2  2  1  2  1
190840  TFT  2  1  2  2  1  2  1
184000   Angel 2  2  2  2  2  2  2
184000   Angel 2  2  2  2  2  2  2
184000   Angel 2  2  2  2  2  2  2
184000   Angel 2  2  2  2  2  2  2
166200   Devil  1  1  1  1  1  1  1
=====

Generation 5
=====
238550  TFT  2  1  2  2  1  2  1
238550  TFT  2  1  2  2  1  2  1
238550  TFT  2  1  2  2  1  2  1
238550  TFT  2  1  2  2  1  2  1
238550  TFT  2  1  2  2  1  2  1
230000   Angel 2  2  2  2  2  2  2
230000   Angel 2  2  2  2  2  2  2
230000   Angel 2  2  2  2  2  2  2
230000   Angel 2  2  2  2  2  2  2
207750   Devil  1  1  1  1  1  1  1
=====
```

Experiment 5(a).3: 4 TFTs, 5 Angels; Devil invading

```
=====
Generation 1
=====
51240  Devil  1 1 1 1 1 1 1 1
47710  TFT    2 1 2 2 1 2 1
47710  TFT    2 1 2 2 1 2 1
47710  TFT    2 1 2 2 1 2 1
47710  TFT    2 1 2 2 1 2 1
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
=====
Generation 2
=====
102480 Devil   1 1 1 1 1 1 1 1
95420  TFT    2 1 2 2 1 2 1
95420  TFT    2 1 2 2 1 2 1
95420  TFT    2 1 2 2 1 2 1
95420  TFT    2 1 2 2 1 2 1
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
=====
Generation 3
=====
153720 Devil   1 1 1 1 1 1 1 1
143130 TFT    2 1 2 2 1 2 1
143130 TFT    2 1 2 2 1 2 1
143130 TFT    2 1 2 2 1 2 1
143130 TFT    2 1 2 2 1 2 1
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
=====
Generation 4
=====
204960 Devil   1 1 1 1 1 1 1 1
190840 TFT    2 1 2 2 1 2 1
190840 TFT    2 1 2 2 1 2 1
190840 TFT    2 1 2 2 1 2 1
190840 TFT    2 1 2 2 1 2 1
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
=====
Generation 5
=====
256200 Devil   1 1 1 1 1 1 1 1
238550 TFT    2 1 2 2 1 2 1
238550 TFT    2 1 2 2 1 2 1
238550 TFT    2 1 2 2 1 2 1
238550 TFT    2 1 2 2 1 2 1
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
=====
```

Experiment 5(a).4: 3 TFTs, 6 Angels; Devil invading

```
=====
Generation 1
=====
60930  Devil  1 1 1 1 1 1 1 1
47710  TFT    2 1 2 2 1 2 1
47710  TFT    2 1 2 2 1 2 1
47710  TFT    2 1 2 2 1 2 1
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
46000  Angel   2 2 2 2 2 2 2 2
=====
Generation 2
=====
121860 Devil   1 1 1 1 1 1 1 1
95420  TFT    2 1 2 2 1 2 1
95420  TFT    2 1 2 2 1 2 1
95420  TFT    2 1 2 2 1 2 1
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
92000  Angel   2 2 2 2 2 2 2 2
=====
Generation 3
=====
182790 Devil   1 1 1 1 1 1 1 1
143130 TFT    2 1 2 2 1 2 1
143130 TFT    2 1 2 2 1 2 1
143130 TFT    2 1 2 2 1 2 1
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
138000 Angel   2 2 2 2 2 2 2 2
=====
Generation 4
=====
243720 Devil   1 1 1 1 1 1 1 1
190840 TFT    2 1 2 2 1 2 1
190840 TFT    2 1 2 2 1 2 1
190840 TFT    2 1 2 2 1 2 1
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
184000 Angel   2 2 2 2 2 2 2 2
=====
Generation 5
=====
304650 Devil   1 1 1 1 1 1 1 1
238550 TFT    2 1 2 2 1 2 1
238550 TFT    2 1 2 2 1 2 1
238550 TFT    2 1 2 2 1 2 1
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
230000 Angel   2 2 2 2 2 2 2 2
=====
```