

Chapter 3

Chapter 3A: ESS in two easy lessons

The purpose of this chapter is to review some classical examples of evolutionary game theory models for behavior and life-history traits, and give an indication of how they can be analyzed using the idea of an Evolutionarily Stable Strategy. Evolutionary game theory is now a vast subdiscipline of theoretical ecology and this chapter is an ultra-minimal introduction. For a broader view of the many current applications of evolutionary game models, a good starting point is the volume edited by Dugatkin and Reeve (1998).

First some motivation. The reason for needing a different approach to individual adaptation is *frequency dependence*, meaning that the costs and benefits of a particular action or trait depend in part on the actions or traits of other individuals in the population. A consequence of frequency dependence is that evolution is not expected to produce optimality in any absolute sense. As a simple example to show why this is true, consider a simple 1-locus, 2-allele model for gene frequency change in a randomly mating diploid population with constant population size. Let A and a denote the 2 alleles, $p(n)$ the frequency of allele A in generation n , and W_{AA}, W_{Aa}, W_{aa} the genotype fitnesses. We don't need to analyze (or even to fully write down) this model. All we need is one result about the model: if $W_{AA} > W_{Aa} > W_{aa}$ in generation n , then $p(n+1)$ will be higher than $p(n)$.

Now suppose that the genotype fitnesses have the following frequency dependence:

$$W_{AA} = 5 - 5p, \quad W_{Aa} = 4 - 4p, \quad W_{aa} = 3 - 3p. \quad (3.1)$$

Then the frequency of allele A always increase from generation to generation (unless it is already at frequency 1), so the population converges onto $p = 1, W = 0$ – which is the lowest possible fitness. Things aren't always this bad. But this example shows that when there is frequency dependent fitness for a trait or behavior, we can't use optimality principles to predict the outcome of evolution.

3.1 Lesson 1: Hawks and Doves

The canonical example of an evolutionary game model is Hawk-Dove model for pairwise conflicts between individuals. This was motivated originally by the question of why animal conflicts are often settled without full-scale battle between the individuals, e.g. males resolving contests over mates without either being greatly harmed by the other.

Maynard Smith and Price (1972) proposed a simple model for pairwise contests in the framework of noncooperative game theory. They assume that pairs of individuals are drawn at random from the population, and contest for some item of value V . Each individual has the choice of two behaviors: they can Display (a show of strength without actual attack) or Escalate (a real attack on the other individual). If both individuals Display, then the item goes to one of them chosen at random. If one displays and the other Escalates, the latter gets the item. If both Escalate there is a fight (with cost c to both participants), and at the end the item goes to one of them chosen at random. The behavioral choices by the two individuals are assumed to occur simultaneously – meaning that each must decide without knowing what the other will do (most models in evolutionary game theory have made this assumption, but can also consider games with multiple rounds where each decision can depend on what the players have done previously).

We can summarize the model by writing down the expected “payoff” to an individual its own behavior and that of the other member of the pair. Let $W(X, Y)$ denote the payoff to an individual with behavior X paired with an individual with behavior Y . The model is then summarized by the payoffs:

$$W(D, D) = V/2, \quad W(D, E) = 0, \quad W(E, D) = V, \quad W(E, E) = V/2 - c.$$

These can be represented in the *payoff matrix*

	Display	Escalate	
Display	$V/2$	0	(3.2)
Escalate	V	$V/2 - c$	

Entries in the matrix are the payoff to the individual using the behavior on the left, if its opponent uses the behavior at the top. All decisions depend on relative payoffs – differences between entries in the matrix – so nothing changes if a constant is added to each entry in the matrix. So don’t be worried about the possibility of negative fitness (less than zero offspring?) – the entries in the matrix should be thought of as modifications to some baseline fitness W_0 , where $W_0 + (\text{any matrix entry})$ is positive.

The language being used to describe the model reflects the roots of game theory in economics. In applying these models to behavior, a tacit assumption is that the “reward” or “payoff” translates into individual Darwinian fitness. Individuals are then assumed to behave so as to maximize their expected payoff.

Frequency-dependent fitnesses result from the fact that the expected payoff for a given behavior depends on what others in the population are doing. For example, suppose first that the population is dominated by Hawks, individuals who always escalate. Then an individual who Displays gets payoff $W(D, E) = 0$,

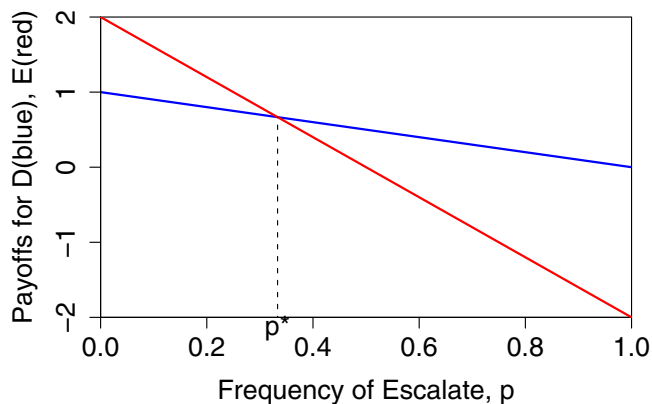


Figure 3.1: Graphical representation of the finding the ESS mixture for the Hawk-Dove game when $V/2 - c < 0$. Note that this is qualitatively like the example (3.1), in that a higher frequency of Escalation decreases the mean payoff from all strategies. The ESS mixture p^* does not optimize fitness at either the individual or population levels.

and one who Escalates gets payoff $W(E, E) = V/2 - c$. If $V/2 - c > 0$, then the best option for the focal individual is to Escalate. The Escalate strategy is then an *Evolutionarily Stable Strategy*, or ESS – given that everyone else does it, you ought to do the same. But if fights are very costly so that $V/2 - c < 0$, the always-Escalate strategy is not an ESS, because an invading mutant who chooses to Display gets higher fitness.

In contrast, the always-Display strategy cannot be an ESS. If the population is dominated by Doves who always Display, then an individual who Displays gets $W(D, D) = V/2$ while one who Escalates gets $W(E, D) = V$, which is greater.

So the interesting situation is when fights are costly, $V/2 < c$, so neither Dove (always Display) or Hawk (always Escalate) is an ESS. What then?

Well, it depends. We have to decide whether individuals are stuck playing one of the *pure strategies* Hawk, Dove – meaning that each individual uses the same behavior on each encounter with another individuals – or if they can play a *mixed strategy*, doing different things on different occasions. In either case, however, the prediction is a mixture of strategies at the population level. Specifically, an evolutionarily stable population state must have the property that in any one play of the game, the expected payoffs for Display and Escalate must be equal. For if not, say if there was a higher payoff for Display, the best choice for an individual would be to always Display – so the population state could not really have been stable after all, because the frequency of Display would increase as a result of higher fitness for that behavior.

To find the stable mix, let p be the population frequency of the Escalate behavior. That means that

an individual's opponent has probability p of Escalating, probability $1 - p$ of Displaying. The expected payoffs for the individual's options are then

$$\begin{aligned} W(D, pE + (1 - p)D) &= pW(D, E) + (1 - p)W(D, D) = (1 - p)(V/2) \\ W(E, pE + (1 - p)D) &= pW(E, E) + (1 - p)W(E, D) = p(V/2 - c) + (1 - p)V \end{aligned} \quad (3.3)$$

The stable mix p^* is then found by setting these equal,

$$(1 - p^*)(V/2) = p^*(V/2 - c) + (1 - p^*)V$$

giving the nice prediction

$$p^* = \frac{V}{2c}. \quad (3.4)$$

(see Figure 3.1). That is, if the cost of a fight is high relative to the value of the item being contested, your frequency of escalating to a fight should be low – just high enough to deter others from assuming that you won't ever fight, so they might as well Escalate and take the item at no cost to themselves.

The attractive feature of the ESS concept is that you don't have to say anything about the genetic basis for the trait, or about the dynamics of gene-frequency change. Everything is strictly in terms of the payoff function. An ESS strategy is defined strictly by the property that “cheaters don't prosper” – if everyone else in the population is behaving according to the ESS, then you can't get a higher payoff than the others by moving to some other strategy.

Exercise 3.1 A parental care game (based on a book in preparation by R.A. Johnstone and D.J.D. Earn). Each “round” of this game is played by two parents who simultaneously face the same decision: whether to remain and **Care** for the young they have produced together, or to **Desert** the brood and seeking a new mate. Assume that there are n offspring in a brood. If both parents Care, a proportion s_2 of these offspring will survive. If only one parent stays and the other Deserts, the proportion of young surviving will be $s_1 \leq s_2$. If both parents Desert, offspring survival will be $s_0 \leq s_1$. A parent that Deserts has a probability m of finding a second mate, with whom it can produce a second brood of n offspring, of which a proportion s_L survive.

(a) Let $W(x, y)$ denote the payoff to a parent with behavior x when the other parent has behavior y , $x, y \in \{C, D\}$ standing for **Care, Desert**. Explain in words why the model's assumptions lead to the following expressions for the payoffs:

$$W(C, C) = ns_2 \quad W(C, D) = ns_1 \quad W(D, C) = ns_1 + mns_L \quad W(D, D) = ns_0 + mns_L \quad (3.5)$$

- (b) Under what conditions on the parameters is **Care** an ESS?
- (c) Under what conditions on the parameters is **Desert** an ESS?
- (d) Can **Care** and **Desert** both be ESS's, and if so, when?
- (e) Under what conditions will neither **Care** nor **Desert** be an ESS, and what is the predicted evolutionary outcome then?

3.2 Lesson 2: sex allocation in hermaphrodites

One of the earliest applications of “ESS thinking” – long before ESS’s were named, and possibly known to Darwin – was to the evolution of sex ratios: what proportion of offspring should be male versus female? A more recent extension, and one that has made considerable contact with data (see the inspiring book by Charnov (1982)), is sex allocation by hermaphroditic species (such as plants that produce both pollen and ovules) to male versus female “function” (modes of reproduction). To find the ESS allocation, we consider a population dominated by a resident type with a particular allocation to male and female function, and compute the fitness of a rare invader with a different allocation. The simplest model goes like this:

- Nonoverlapping generations, with adults diploid and gametes haploid, and a constant population size (number of adults), N .
- Resident adults produce F gametes through female function, and M gametes through male function.
- The next generation is formed by random mating of gametes.

We can compare different allocation strategies based on the number of gametes that an individual contributes, on average, to the next generation. The resident population produces NF gametes through female function, each of which mates with a gamete produced by male function *by some resident* (because the population is dominated by the resident type), to produce NF zygotes containing a total of $2NF$ resident gametes. To maintain population size, the survival probability of zygotes must be $1/F$ to produce a total of N adults in the next generation. The N resident adults therefore put $2NF/F$ gametes into the next generation, for an average of 2 gametes per resident adult. (There’s a quicker but less instructive route to this conclusion: there are $2N$ gametes in the next generation, all produced by residents, so on average each of the N adults in the previous generation contributed 2 gametes to the next generation.)

Now consider one rare invader. By female function it produces F_i gametes. Each of these mates with a resident’s male-function gamete, yielding F_i zygotes. The zygote survival is $1/F$, so this invader puts (on average) F_i/F gametes into the next generation through female function. By symmetry (male and female are just names in this model, and they could be interchanged without changing any assumptions), the invader puts M_i/M gametes into the next generation through male function. So the invader puts a total of $M_i/M + F_i/F$ gametes into the next generation. The ESS allocation M^*, F^* therefore has the property that

$$\frac{M_i}{M^*} + \frac{F_i}{F^*} < 2 \text{ for all } (M_i, F_i) \neq (M^*, F^*). \quad (3.6)$$

This is known as the *Shaw-Mohler* equation. To give it a more intuitive interpretation, let p denote the fraction of resources put into male function, so that M and F are functions of p . The Shaw-Mohler condition is that

$$W(p, p^*) = \frac{M(p)}{M(p^*)} + \frac{F(p)}{F(p^*)} < 2 \text{ for all } p \neq p^*. \quad (3.7)$$

Because $W(p^*, p^*) = 2$, the ESS p^* must have the property that

$$\frac{\partial W}{\partial p}(p, p^*) = 0 \text{ when } p = p^*.$$

That is,

$$\frac{M'}{M} + \frac{F'}{F} = 0 \Rightarrow M'F + F'M = 0 \Rightarrow (MF)' = 0 \quad (3.8)$$

where $'$ indicates the derivative with respect to p . The ESS allocation to male versus female reproductive functions therefore maximizes the product of the numbers of viable gametes produced through male and female functions.

Exercise 3.2 Modify the reasoning above so that it applies to single-sex individuals (each individual is either male or female) in order to derive the ESS sex ratio of offspring as a function of the cost for producing viable male versus female offspring. The “map” from the hermaphrodite model to sex-ratio calculations is as follows: Instead of male-function and female-function gametes, consider male and female offspring. Instead of counting gametes in the next generation, count grandchildren. As a special case, show that a 50:50 sex ratio is optimal if male and female viable offspring are equally costly.

Exercise 3.3 Selfing: suppose that a fraction s , $0 \leq s \leq 1$ of each adult’s female-function gametes are fertilized by male-function gametes produced by the same individual (i.e. they are self-fertilized), and that male-function gametes are so cheap relative to female (e.g. pollen vs. ovules in plants) that a negligibly small fraction of the individuals male-function gametes are sufficient to mate all of the female-function gametes. If $s = 1$, the ESS is clearly $M = 0, F = 1$. Derive the conditions defining the ESS allocation to M as a function of s and show that it is generally a decreasing function of s .

3.3 Proceed with caution

As noted in the last chapter, the ESS approach is an attempt to shortcut through many details (such as: how are behavioral traits inherited?) and get straight to a prediction. The examples in this chapter highlight one shortcut in particular. The stability concept for an ESS is that once the population is at the ESS, there is no benefit for a change in strategy. This says nothing about whether or not the population would ever get to the ESS (a property called convergence stability): if the population is close but not quite (e.g., a mix of Hawks and Doves in some proportion $p \approx p^*$) will evolution move the population closer to the ESS? The answer to that question, unfortunately, depends on the specific payoff function. The answer can be “no”, so a population near the ESS can be invaded by individuals further from the ESS but not by individuals closer to it. The answer may also depend on which model is adopted for the evolutionary dynamics of strategies – exactly how does a difference in current payoffs translate into a change in behavioral strategies from one generation to the next? Finally, one really needs to be careful about checking second-order (i.e. second-derivative) conditions for a maximum. A purported ESS identified by a first-derivative condition such as (3.3) or (3.8) might turn out to be a fitness *minimum* rather than a maximum. And it can even turn out – if you rig things just right – that a

population can converge to a strategy that (once the population gets there) is a fitness minimum rather than a fitness maximum.

These are still murky and contentious waters, as can be seen in (for example) Waxman and Gavrillets (2005) and the responding articles in that issue of *Journal of Evolutionary Biology*. As Waxman and Gavrillets review, first-order conditions on an appropriate payoff function define an *Evolutionarily Singular Strategy* – calling this an ESS has become established usage but it’s such a *really* bad idea that we will call it an ESIS instead. Any ESS has to be an ESIS, but an ESIS might not be an ESS. Many of the questions raised in the last paragraph can be settled by looking at the second derivatives of the payoff function at the ESIS. For example, let $r(v, u) = W(v, u) - W(u, u)$ be the relative payoff in Hawk-Dove for an individual who escalates with probability v , in a population where the resident strategy is to escalate with probability u . A v -type invader will increase in frequency if $r(v, u) > 0$. An ESIS p^* in this setup is defined by the property that $\frac{\partial r}{\partial v} = 0$ at $v = u = p^*$. The predicted evolutionary outcome depends on the second derivatives of r at p^* . Figure 3.3, lifted from Levin and Mueller-Landau (2000) is a nice summary of the many possibilities. The key thing to notice is that non-invasibility (the property defining an ESS) does not exactly coincide with convergence stability. So a population may fail to converge to an ESS, or it may converge to an ESIS that is not an ESS. How important this is for understanding behavioral evolution remains to be seen.

3.4 References

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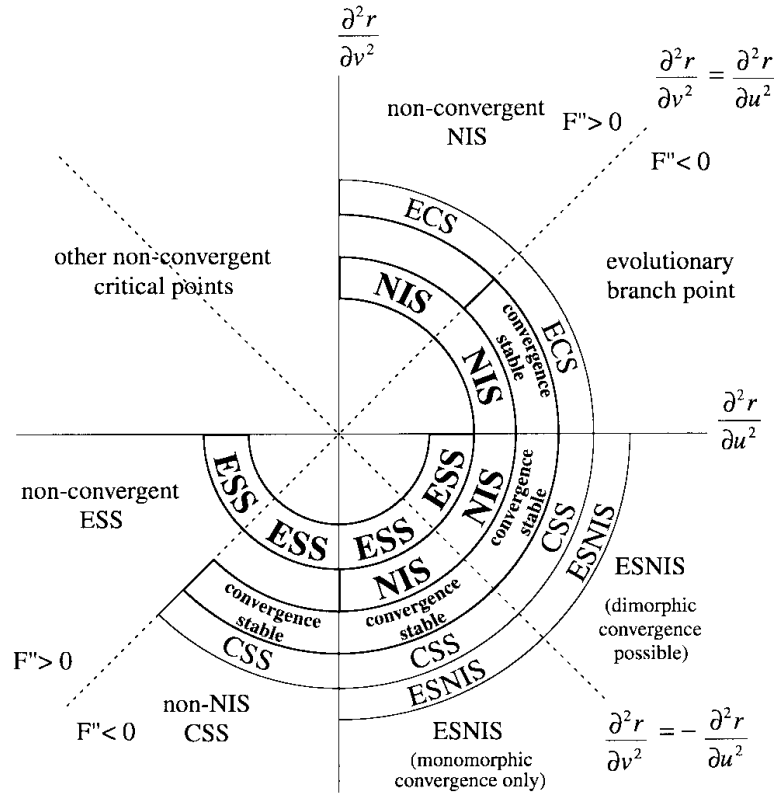


Fig. 1. Classifications of the properties of critical points of the fitness function, r , in terms of their pure second partial derivatives with respect to the type of the resident, u , and of the invader, v . ESS = evolutionarily stable strategy; NIS = neighbourhood invader strategy; CSS = continuously stable strategy; ECS = evolutionarily compatible strategy; ESNIS = evolutionarily stable neighbourhood invader strategy. Note that the points to the right and below the line where the two derivatives are equal (convergence stable points) are ones for which the function F has a maximum.