BIO 45 – Lect., II_6 & 7 -- ESS THEORY and GAME THEORY MODELS

I. Game Theory - Another Cost/Benefit Way Of Thinking

Let's explore the expected "design" of animal contests – one "flavor" of communication. Besides "who wins and why", there are two basic questions about animal contests: (1) why are contests ritualized and usually settled by display rather than fighting? and (2) why do some contests escalate into physical struggles or all out fights? These questions have been around for a while and have had answers (1. = for the good of the species, 2. = mistakes, or controlling for cheating).

Since physical struggles are risky and cost a lot of energy, selection should favor ways to settle disputes by a means of assessing who would be likely to win if there were to be a physical struggle. Displaying information that allows the contestants to make such assessments should then be the general means for settling contests. Escalated, physical fights should occur when contests can't be settled by such a display or when one contestant is "checking-up on the other". Game theory models formalize this conceptual thinking. We seek a way to determine what the best tactic or set of tactics is for a given contest situation. We define a currency (fitness gain and loss) and a utility function to be maximized (fitness gain per unit of time). We use the models to determine how various tactics should do in pair-wise contests (what are the relative payoffs for each tactic against itself and the others). We ask, "Is there a best tactic for a given kind of contest? We call that tactic (or set of tactics) the ESS or Evolutionarily Stable Strategy.

ESS = a behavioral strategy (one or more tactics) which, once common in a population, cannot be invaded or replaced by another strategy (tactic). The alternative tactics are stated as part of the model, so an ESS is not "stable against every possible tactic". Clearly evolution is not stable in the sense of not changing. The ESS is for a specific problem (game) and a given set of existing or plausible tactics and their associated payoffs. Given these payoff values (costs and benefits) the model shows which tactic is stable or if there will be equilibrium of more than one tactic. If conditions change, then so may the resulting ESS.

Unlike optimality theory, ESS models usually involve direct interactions between different types of individuals in the same population. There is some overlap between optimality and ESS theories, but I will stress the divergent ways of thinking that can result. We will examine ESS games in the context of animal contests where the costs are energy, time and risk of injury and gains are resources (the currency used to approximate fitness units). There are two basic kinds of contests -- symmetric and asymmetric. Symmetric contests are ones in which the contestants enter the contest with no positional advantage or anything other than their tactics. The outcome depends on the relative payoffs for the tactics when used against each other. You were in a symmetric contest if you ever played "paper stone and scissors" or "odds and evens". Each person chose what they would do and the other had no way of telling which tactic (odd - even) they would face until it happened. Hawk vs. Dove games discussed below are symmetric.

Asymmetric contests are ones where there is an initial difference between opponents that gives one an advantage over the other. For example, if the contest is over a territory and involves the resident and an intruder the resident may have an advantage. Such a contest might involve a display of residency at which point the intruder may leave. Other asymmetries are things like size, strength or weapons. Our examples of asymmetric contests will be territorial disputes in damselflies (next lecture) and red deer contests (see Alcock).

II. Game Theory Models -- a simple example

The "hawk vs. dove" model that follows is not a model of a real situation in nature. Instead it is a heuristic model for a way of thinking. There are newer and more sophisticated versions of ESS models. Recent ESS models examine questions like the effects of assessment during contests, male-female interactions, sex ratio adjustment and life history tactics. We will stay with the basic models.

Let's say there are two kinds of tactics in a population, one (**hawk**) that always fights for a resource and one (**dove**) that shares with each other and runs away from hawks. Are there any conditions under which these two tactics can coexist or is one tactic better than the other? Imagine a population of **hawks** and **doves** moving about at random. They come together at a pile of food that is worth some value (V). We need to determine who gets the food for each possible kind of encounter (H vs. H, D Vs D and H Vs D).

We can model the problem with a payoff matrix (next page). In the top row are the opponents and in the side column is who we are focused on. The cells in the table describe the outcome of the interactions. When a hawk bumps into a dove (upper right cell) the dove runs away and the hawk gets V. When a dove encounters a hawk (lower left) it runs away and gets nothing (0).

When a dove meets a dove they split the food so our dove gets V/2. Finally, when a hawk meets a hawk they both fight. We could make a variety of formulae for this cell (upper right) but let's just say that they fight at some cost (C) and each has an even chance of winning. So the result for our hawk fighting another hawk is the food minus the cost of fighting (V-C) divided by 2 (the chance of winning). The payoff matrix can then be solved mathematically.

Hawks and Doves Model for C<V

Hawk = always fights
V = resource value

Dove = shares with dove, runs from hawk
C = cost of injury from fighting

Payoff Matrix formulae

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

Payoff Matrix with V = 4 & C = 2

Versus ➔	Hawk	Dove
Hawk	1	4
Dove	0	2

We, however, can explore our payoff matrix for a solution (which tactic is best) by looking at two things: 1) can Dove invade a pure population of Hawk?, 2) can Hawk invade a pure population of Dove? The answers here (if V = 4 and C = 2) are no and yes. In a pure population of Hawks the average pay-off is 1 (all contests are H Vs H). The payoff for Dove Vs Hawk (lower left) is 0, which is less than 1, so Dove cannot invade. Likewise a pure population of Dove has an average pay-off of 2, which can be invaded by hawks (H Vs D = 4). So only one can invade the other and it will be a pure ESS -- all Hawk.

Take another look at our payoff matrix. What is the average payoff to individuals in a population of hawks? What would it be if the population was made up entirely of doves? This is a valuable insight from these models. A “good for the species” view would say it is best to all be dove. But dove is prone to invasion by a more selfish tactic -- hawk.

Interestingly, for some values of V and C only hawk is the ESS, but for other values there is an equilibrium proportion of hawk and dove. How can that happen if we just showed that hawk always invades and takes over dove populations? The answer has to do with costs and benefits of fighting. For example, what happens when V = 2 and C = 4? Play with our payoff matrix for these values and then turn the page.

The ESS for **costly** contests is a Hawk/Dove equilibrium (when C > V, e.g., C=4 and V=2). Remember, we can tell if a pay-off matrix will result in an equilibrium by looking at two things: 1) can Dove invade a pure population of Hawk?, 2) can Hawk invade a pure population of Dove? The answers here are yes and yes. In a pure population of Hawks the average pay-off is -1 (all contests are H vs. H). The payoff for Dove vs. Hawk is 0 which is greater than -1, so Dove can invade. Likewise a pure population of Dove has an average pay-off of 1 which can be invaded by hawks (H Vs D = 2). So they both can invade each other and neither can be a pure ESS. In fact you can demonstrate the equilibrium by starting with a population of 50% Hawk and 50% Dove. That means that half the contests a Dove has are with Hawk (= 0) and half are with Dove (= 1). Thus the average pay off to Dove is 0.5 (0 + 1 / 2). What is the average pay off to Hawk in a 50:50 population. You can play with these percentages to convince yourself that no matter what proportion of Hawk and Dove you start with the population will end up at 50:50 -- the point at which Dove and Hawk "fitness" is equal. Different values of C and V will give different equilibrium proportions as long as C > V. If you have a spreadsheet program, you can set up the payoff matrix in that program and play with different values of V and C and with different starting conditions to get a better sense of the dynamics of the model.

Hawks and Doves Model for C>>V
V = 2 C = 4

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

Versus ➔	Hawk	Dove
Hawk	-1	2
Dove	0	1

III. General Insights From The ESS Way Of Thinking:

1. **Success** (fitness gain) of a behavioral tactic or variant **will usually depend on the nature** (V and C payoff matrix) **and relative abundance of other tactics** -- how well you do using behavior X depends on what others are using and how many there are relative to your tactic. This is the basic idea of 'frequency dependence'.

2. **Rather than there always being one optimal or best behavior, for a given situation, two or more behaviors <u>may</u> coexist in a stable equilibrium** -- as polymorphism in population, or as alternative tactics employed by single individuals. Stable means they have equal fitness.