

# Evolutionary Game Theory

## Introduction:

This chapter discusses evolutionary game theory. Other game theory strategies analyze simultaneous decision making reasoning based on what the other players might do. This branch of game theory focuses on decisions by players with no reasoning behind it. Within this chapter, the examination of the field of origin for evolutionary games will first be discussed, followed by its methodology, main features, and real-life applications of evolutionary game theory within biological systems.

## Economics and Biology

Economics and biology have certain features in common and there have been interactions between them. There is a basic parallel between economics and sociobiology: the study of behavior of actors and survival of those actors in an external environment marked by competitive processes.<sup>1</sup> Evolutionary game theory originated from the field of evolutionary biology, which is based on the idea that an organism's genes largely determine its observable characteristics, and hence fitness within its environment.<sup>2</sup> Organisms that are more fit will tend to increase their representation in the population. Through this mechanism, fitter genes tend to win over time, because they provide higher rates of reproduction.

The basic postulate in economics is utility maximization. Humans, governments, and firms have the objective of maximizing their

corresponding preferences. The biological counterpart is as many genes or animals of a certain species will be reproduced in subsequent generations in order to maintain their survival in the long-run, known as reproduction survival. Hirshleifer (1977) created the table below to explain how these two disciplines intertwine.

	Economic	Biological
Objective Function:	Preferences	Survival
Principle of Action:	Optimization	"As-of Optimization
Opportunities:	Production	Resource exploitation
	Market Exchange	Mutualism
	Crime, war	Predation, war
	Family Formation	Reproduction
Competitive Selection:	Economic Efficiency	Superior Fitness
Equilibrium:		
Short-Run	Market Clearing	?
Long-run	Zero-profit	Reproductive ratio = 1
Very long-run	Stationary state	Saturated environment
Progress:	Accumulation Technological advance	Evolution
	Institutional change	

Table 1. Processes and Relationships (Hirshleifer, 1977)

Within biological boundaries, evolutionary game theory is a way of thinking about evolution at the phenotypic level when fitness of particular phenotypes depends on their frequencies in their population. To maintain survival or preferences and reproduction the economic and biological systems have different opportunities. In general economics, survival is based on manufacturing

1 ~~\_\_\_\_\_~~ ?  
 2 ~~\_\_\_\_\_~~

goods or generating services and subsequently exchanging these goods and services on the market and in biological systems, reproductive survival could be secured by means of resources exploitation, mutualism, predation, war, and reproduction.<sup>3</sup> The biological analogy of economic efficiency could be that behavioral fitness of a particular organism is superior relative to its direct competitors. Now that the connection between biology and economics has been discussed, the next section explains the basic foundation and components of evolutionary game theory.

### Basic Foundation of Evolutionary Games

Unlike simultaneous games where each player makes a decision based on their prediction on what the other player will play, evolutionary games shows that basic ideas of game theory can be applied even to situations in which no individual is overtly reasoning or even explicitly making decisions.

**Evolutionary Games:** *the application of game theory to evolving populations within biological systems. Evolutionary game theory is useful within this context by defining the framework of contests, strategies, and analytics of the Darwinian competition model.*

The basic area of study for evolutionary games is different behaviors that have the ability to persist in populations and which forms of behavior have the tendency to be driven out. Within biological boundaries, evolutionary game theory is a way of thinking about evolution at the phenotypic level when the fitness of particular phenotypes

### Components of Evolutionary Games:

- **Strategies:** organism's (player's) genetically determined characteristics and behaviors.
- **Payoffs:** fitness – depends on the strategies (characteristics) of the organism it interacts with.

depend on their frequencies in the population (Maynard Smith, 1982, p.1)

Like any other form of game theory, evolutionary games must have a specific setup.

There are two important components of evolutionary games:

1. Strategies are not chosen by the organism, rather it is chosen for them as it is genetically hardwired into their systems.
2. Many behaviors involve the **interaction** of multiple organisms in a population and the success if any one of these organisms depend on how its behavior interact with that of others.

***Fitness of an individual cannot be measured in isolation – rather, it has to be evaluated in the full population in which it lives in.***

Below is a formal model of strategic interactions over time in which:

- A. Higher payoff strategies tend to displace lower payoff strategies over time.
- B. But there is some inertia (resistance to any change) and
- C. Players do not systematically attempt to influence other player's future actions.

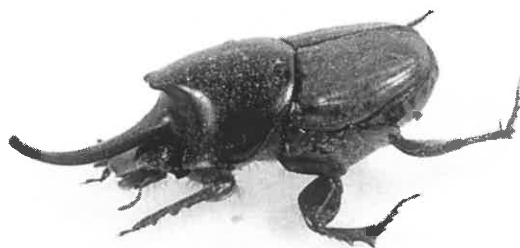
The condition (A) above is a version of the "survival of the fittest" concept and condition (B) distinguishes evolutionary change from revolutionary change and explains that aggregate behavior does not change too quickly. Finally, condition (C) represents the game against Nature condition (GAN) and this

separates evolutionary games from repeated games with trigger strategy threats.

With that basic foundation of evolutionary games explained, in the next section, the importance of fitness of this type of game theory will be explained with a real-life example.

**Fitness is the Result of Interactions between organisms of a biological systems**

To understand how game theory strategies relate to evolutionary biology, fitness is measured between species to determine payoffs. Fitness is the payoffs species receive from interactions with other species. This payoff depends on the strategies of the organisms with which it interacts. Fitness levels are illustrated with a game matrix. Let's use a real life example to explain how fitness can be laid out.



The Dung beetle, found primarily in Egypt is a species whose survival depends on its size. These organisms eat the feces of herbivores and omnivores. Certain mutations however can create large and small dung beetles. For this type of beetles, fitness is determined largely by the extent to which it can find food and use nutrients efficiently. For this example, the mutation created a larger type of beetle. The larger body leads to a higher difficulty in maintaining metabolic requirements, which is a *negative effect on fitness*.

Within specific environments, large and small dung beetles compete with each other for food. Within the game matrix below, fitness of payoff is determined by the amount of food they receive. There are three possible outcomes that can happen when beetles interact with each other for food.

1. When beetles of the same size compete, they get the same amount of food (equal payoff).
2. Large vs. small beetles leads to the larger beetle getting more food (higher payoff).
3. In all cases, the large beetles experience less payoff from a given quantity of food since they have higher metabolic rate. Therefore two large beetles interacting will have a lower payoff than two small beetles interacting.

Below is a game matrix to illustrate the conditions above.

Figure 1.

		Beetle 2	
		S	L
Beetle 1	S	5,5	1,8
	L	8,1	3,3

S = small and L = Large

Figure 1 indicates that the larger beetle always receives a higher payoff when it plays a smaller beetle. When two larger beetles meet each other, they both receive a lower payoff than when two small beetles play each other because of the higher metabolic rate. the overall fitness of a phenotype is

equal to the average fitness from each of its pairwise interactions with others. This will determine the reproductive success – the number of offspring that carry its gene (hence strategy) into the next generation.

*A key point is that the beetles are not choosing the strategy they end up playing. They're genetically hardwired to play one their entire life.* Now that the game has a visual setup, Nash Equilibrium and Evolutionary stable strategies will be discussed.

**Nash Equilibrium and Evolutionarily Stable Strategies**

The equilibrium concept that is the foundation for economic theory is Nash Equilibrium – a strategy profile such that each player is choosing optimally given the expected choice of the other. However, Nash Equilibrium does not apply to evolutionary games for two reasons. First, the players are not choosing their strategies; rather, it is hardwired into them and second, Nash Equilibrium is a static concept and assumes that the game is not repeated over and over again, but in evolutionary games, the game is repeated many times to eliminate a specific strategy throughout subsequent generations.

Within evolutionary games, we are specifically looking at the long-run outcome of a system that is under a non-linear payoff structure. The analogous notion for Nash Equilibrium within evolutionary games is known as *evolutionary stable strategies (ESS)*.

**Evolutionary Stable Strategies (ESS):**

*Genetically determined strategy that tends to persist once it is prevalent within a population. These strategies are hard-wired into the organism and are not independently chosen.*

In a more detailed explanation, an ESS is a stable situation in the evolutionary process and defines the state of the population that is so-called 'non-invadable' by any mutant strategies of a relatively small fraction of the populations.<sup>4</sup> This basically states that the behavior of the mutants will not survive in the long-run. Below is a general description of how ESS works:

**General Concept of ESS:**

A strategy **T** invades strategy **S** at level **X**:

- For a small positive number **X** if an **x** fraction of the underlying population uses **T** and a **1-x** fraction of the population uses **S**.

*Strategy S is evolutionary stable if there is a small positive number Y for S such that, when any strategy T invades S at any level of X where X<Y, the fitness of the organism playing S is strictly greater than the fitness of the organism playing T.*

Now let's apply the concept of ESS to the beetle example previously stated.

**ESS Application to Beetle Game**

		Beetle 2	
		S	L
Beetle 1	S	5,5	1,8
	L	8,1	3,3

S = small and L = Large

We are going to check if the small or large phenotype is evolutionary stable. Let's say that for a small positive number

$x$ ,  $1-x$  fraction uses small and  $x$  fraction uses large. **Whatever strategy is assigned  $1-x$  is the strategy you are testing to see if its evolutionarily stable.** What we do now is take each possible strategy and use its probability ( $x$  or  $1-x$ ) of facing another strategy to determine its expected payoff.

If we assign small phenotype probability  $1-x$ :

**Expected payoff to a small beetle with random interactions with a population**

- With probability  $(1-x)$  it meets a small beetle (S,S) → beetle 1 receives a payoff of 5.
- With probability  $(x)$  it meets a large beetle (S,L) → beetle 1 receives a payoff of 1.

Expected payoff for beetle 1 being small with  $p(\text{small}) = 1-x$ :

$$5(1-x) + 1(x) = \underline{5-4x}$$

**Expected payoff to a large beetle with random interactions with a population**

- With probability  $(1-x)$  it meets a small beetle (S,S) → beetle 1 receives a payoff of 8.
- With probability  $(x)$  it meets a large beetle (L,L) → beetle 1 receives a payoff of 3.

Expected payoff for beetle 1 being large with  $p(\text{small}) = 1-x$ :

$$8(1-x) + 3(x) = \underline{8-5x}$$

It is easy to check that for most values of  $x$ , the expected payoff for the large beetle is greater than the expected payoff of small beetles when  $p(\text{small}) = 1-x$ :

$$8-5x > 5-4x \text{ for most values of } X, \text{ which indicate that } \underline{\text{small is not evolutionarily stable.}}$$

Now to check if large is evolutionarily stable: we assign large beetle the probability  $(1-x)$  and small beetle  $(x)$ .

**Expected payoff to a large beetle with random interactions with a population**

- With probability  $(1-x)$  it meets a large beetle (L,L) → beetle 1 receives payoff of 3.
- With probability  $(x)$  it meets a small beetle (L,S) → beetle 1 receives a payoff of 8.

Expected payoff for beetle 1 being large with  $p(\text{large}) = 1-x$ :

$$3(1-x) + 8(x) = \underline{3+5x}$$

**Expected payoff to a small beetle with random interactions with a population**

- With probability  $(1-x)$  it meets a large beetle (S,L) → beetle 1 receives a payoff of 1.
- With probability  $(x)$  it meets a small beetle (S,S) → beetle 1 receives a payoff of 5.

Expected payoff for beetle 1 being small with  $p(\text{large}) = 1-x$ :

$$1(1-x) + 5(x) = \underline{1+4x}$$

It is easy to check that for most values of  $x$ , the expected payoff for the large beetle is greater than the expected payoff of small beetles when  $p(\text{large}) = 1-x$ :

$$3+5x > 1+4x \text{ for most values of } X, \text{ indicating that the } \underline{\text{large strategy is evolutionarily stable.}}$$

What both these inequalities are saying is that when small is assigned probability  $1-x$ , the fitness of the large beetle is greater than the fitness of the small beetle, but when large is assigned  $1-x$ , the fitness of the large beetle is greater than the fitness of the small beetle.

So what do these conclusions of ESS mean?

1. If a few large beetles are introduced into a population full of small beetles: large beetles will get most of the food and **the small beetles cannot drive out**

**the larger ones therefore, small is not evolutionarily stable.**

2. If a few small beetles are introduced into a population full of large beetles then the small beetles will do badly, losing almost every competition for food and therefore **the large beetles resists the invasion of small beetles and therefore large is evolutionarily stable.**

Next, we will discuss how stability is characterized between monomorphic and polymorphic populations.

### Stability Between Monomorphic and Polymorphic Populations

Monomorphic populations are characterized by a single phenotype within a species; polymorphic populations, on the other hand, are characterized by two or more phenotypes. For the purposes of this book, we will talk about monomorphic populations as having one trait (i.e. strategy) and polymorphic populations as having two or more traits.

Generally, there are two conditions of stability:  $m$ -stability and  $\partial$ -stability. The  $m$ -stability condition outlines the convergence of a population towards a new evolutionary equilibrium due to an initial increase in rare alleles that typically arise from an invading party. The  $\partial$ -stability condition corresponds to the stability of a population at its evolutionary equilibrium *against* the increase of new alleles. The  $\partial$ -stability can also be viewed as a local version of the classic evolutionarily stable strategy (ESS).

For monomorphic populations, stability is characterized by the presence of the  $\partial$ -stability condition; that is, the presence of an ESS inherently constitutes stability. One strategy persists

once it is prevalent in a population. For polymorphic populations, it is a little more nuanced. We will discuss this below.

The creation of a polymorphic population occurs when there exists an evolutionary equilibrium that is convergence stable but not local ESS stable. That is, the introduction of rare alleles "pulls" on a previously established equilibrium in order to create a new one. If stable, then the polymorphic population is characterized by multiple strategies existing in equilibrium and despite substantial differences, earnings are statistically identical.

### Evolutionary Games Across Species

Conventionally, evolutionary games take the same species and analyze different strategies as traits within that species. However, we can also analyze interactions across evolutionary boundaries by re-assigning "strategies" as different species. Within this paradigm, an ESS will determine which of the two species will survive and which will be run into extinction.

An invading, non-native species can supplant a native species through 3 scenarios:

1. A novel evolutionary technology: the invader represents a novel competitor with respect to the recipient community and possesses a novel evolutionary technology that is evolutionarily unavailable to the species with which it competes;
2. An empty niche: where the native community may have fewer species that would exist at its ESS
3. A non-ESS native species: where if a species of a native community has a strategy that is away from its ESS (i.e. not occupying the

peak of the adaptive landscape) then a species with a strategy closer to or on the opposite side of the peak can successfully invade.

Typically, we would model the arrival of an invader as a game that draws attention to potential changes in trait values and population sizes of the invader and native community through each stage of the invasion process: arrival, establishment, and spread/impact. Additionally, we will use a modified version of the standard Lotka-Volterra population model of competition that models a fitness-generating function: the G-function.

G-function: describes the per capita growth and the evolutionary dynamics of a species possessing a particular strategy within a particular environment.

$$G(\mathbf{v}, \mathbf{u}, \mathbf{x})$$

- $\mathbf{v}$  is the heritable traits of the species that are hypothesized to be relevant for their population ecology and species interactions
- $\mathbf{U}$  is a vector that describes different species where  $u_i$  is the strategy value of the  $i$ th species for  $i = 1, \dots, n$ .
- $\mathbf{X}$  is a vector that gives the current population sizes of each species within the community, where  $x_i$  gives the population size of the  $i$ th species whose strategy is  $u_i$ .

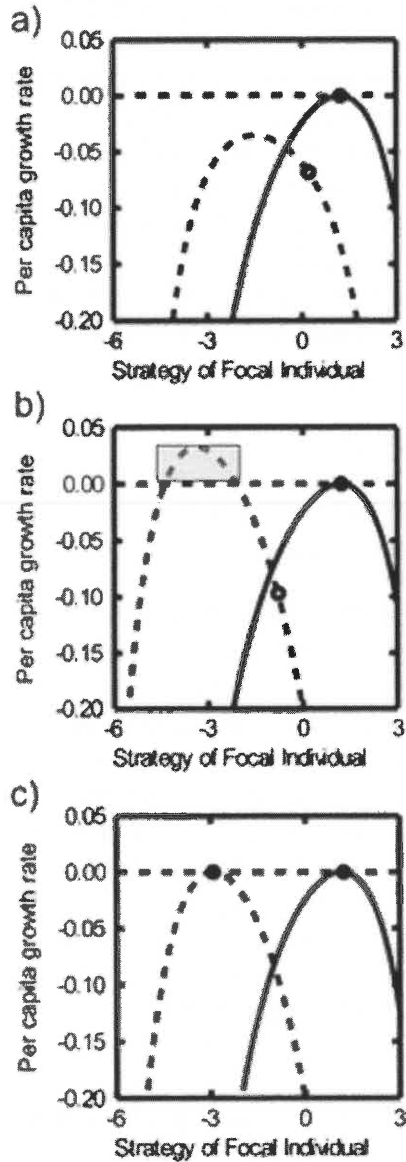
The adaptive landscape of the invader community within the native community determines the ecological (invasion

potential) and evolutionary (invasion window) prospects of invasion; if the invader has a positive invasion potential, then there must exist an invasion window. However, the reverse is not necessarily true: the presence of an invasion window does not mean that the non-native species has a positive invasion potential. Later, we will show how these concepts are represented graphically.

### Novel G-Function

Under this scenario, three general outcomes are possible:

- 1) The invader can arrive with no invasion window and negative invasion potential (Figure 1).
- 2) The invader can arrive with an invasion window but no positive invasion potential. In time, the invasive species will move into a range of positive fitness and positive invasion potential. The possibility exists for the invader to successfully invade, but it requires evolution to rescue the population from extinction (Figure 1).
- 3) The invader can arrive with both an invasion window and positive invasion potential. This will result in an immediately successful invasion. While both species continue to evolve, the non-native species can immediately establish and grow to some positive equilibrium population size. If both species coexist following this establishment, both may coevolve to a new ESS where both occupy new peaks on their respective landscape (Figure 2).

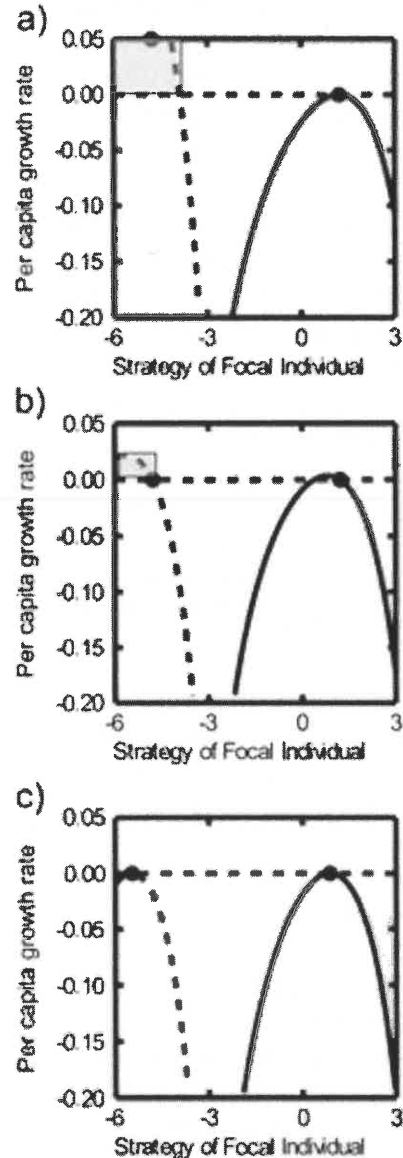


**Figure 1:** An example where the recipient community (*solid line*) is at the threat of an invasion (*dashed line*) with a different G-function (distinct evolutionary technology).

a, the species of the recipient community is at its ESS, the adaptive landscape of the nonnative species offers no invasion window, and the non-native species (*dashed line, black dot*) has negative invasion potential.

b, the adaptive landscape of the non-native species offers an invasion window (*gray box*), but the non-native species (*dashed line, black dot*) starts with negative invasion potential.

c, If the non-native species were able to evolve a strategy within its invasion window, then it would successfully invade and establish a new ESS with both species coexisting.



**Figure 2:** An example where the recipient community (*solid line*) is open to invasion from the current non-native species. The non-native species (*dashed line, black dot*) has a different G-function than the native community.

a, When the species of the recipient community (*solid line, black dot*) is at its ESS, the adaptive landscape of the non-native species offers an invasion window (*gray box*), and the non-native species starts with positive invasion potential.

b, After a successful invasion both species coexist on new population sizes but the community no longer has an ESS.

c, The invading species may evolve to its ESS, making conditions even less favorable for the native species



### Empty Niche

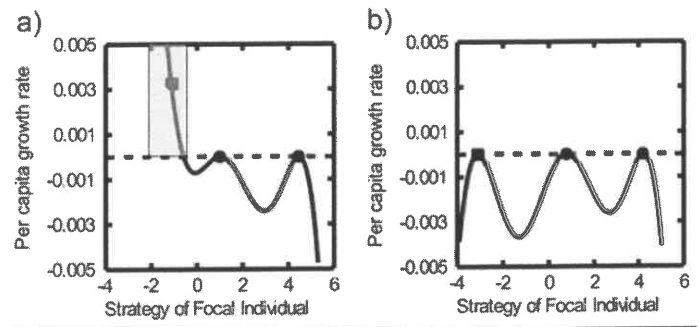
In this scenario, the native species has an invasion window, but the invading species does not necessarily have a positive invasion potential. If they have a negative invasion potential, the invader can either become extinct or evolve into the invasion window. If they arrive with a strategy that falls within the invasion window, the ecologically successful invader is under selection to evolve towards the unoccupied peak. By fulfilling the niche, the evolutionarily stable strategy diversity of species can be filled, with all species occupying their respective peaks, and the community is no longer susceptible to invasion by alternative strategies from within the same G-function (Figure 3).

### Non-ESS Native Community

For native species that do not have an ESS, and the invading species is a part of the same G-function, three outcomes are possible (Figure 4):

- 1) Invader arrives with a strategy that has a negative invasion potential; they are under a lot of pressure to evolve towards the peak of its adaptive landscape. However, invaders will most likely become extinct as the resident species has a "head start" on evolving towards the peak.
- 2) Invader arrives with a strategy that lies between the resident's strategy and the peak, or just on the other side of the peak. The non-native community will rise to its equilibrium. It's not possible for both species to coexist, so the resident species will go extinct.

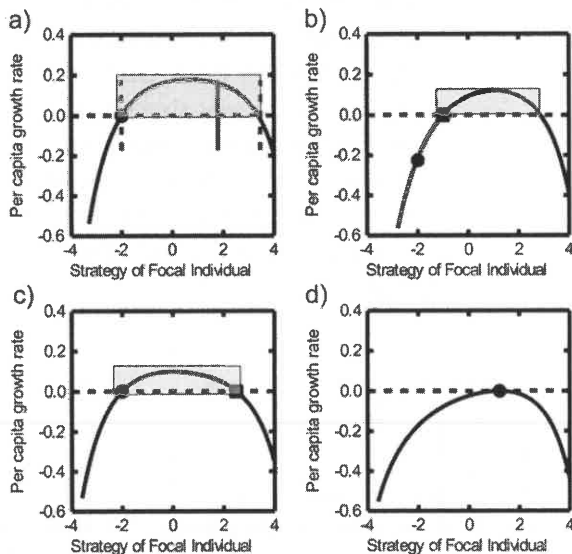
- 3) Invader arrives within the same invasion window and on the opposite side of the peak. Coexistence is ecologically stable, but the new community is not evolutionarily stable as both species are under pressure to evolve towards the same peak. Whichever species reaches the peak first will outcompete the other.



**Figure 3:** An example of an empty niche where the recipient community (*solid line*) has just two species when the ESS would permit three species. This has a single G-function and adaptive landscape.

a, The two species have evolved to local peaks of the landscape, but there is a large invasion window and the opportunity for a non-native species (*black box*) with a positive invasion potential.

b, Following this invasion a new ecological equilibrium exists with all three species coexisting. The ESS diversity of species can be filled with all species occupying their respective peaks. This community is no longer invadable by alternative strategies from within the same G-function.



**Figure 4:** An example of species replacement or coexistence when the species of the native community is not at its ESS.

a, when the native species (*black dot*), is not at its ESS, there exists a positive invasion window (*gray box*).

b, a non-native species (*black box*) that invades with a strategy between the solid and dashed lines will result in species replacement.

c, a non-native species with a strategy between the dashed and solid lines will result in species addition and new ecological equilibrium for the two-species system. However, this community is not evolutionarily stable as both are under selection to evolve towards the same peak.

d, neither the species replacement or addition is an ESS, so evolution should result in convergence on the single-species ESS.

Questions:

- 1) What are the two conditions of stability for analyzing stability in monomorphic and polymorphic populations?
- 2) Will the recipient population be driven to extinction in the empty niche scenario? Why or why not?
- 3) What are the two requirements that must be fulfilled before we can analyze whether or not an invading species will be successful in overtaking the recipient community?
- 4) What are the two main components of evolutionary games?

1. Hummingbirds have created a mutation over generations to help them get more food from different types of flowers. Certain flowers have long stems and the food they provide the birds are lower within their cavity. Over generations, some hummingbirds have developed longer beaks in order to access more food. Below are some of the components for this evolutionary game:

- Hummingbirds compete with each other for food sources.
- Hummingbirds with longer beaks have a greater fitness level because they are able to access more food.
- Short vs. long = (2,2)
- Short vs. long = (1,5)
- Long vs. short = (5,1)
- Long vs. long = (4,4)

- a. Draw a game matrix for this game.
- b. Test to see whether the short-beak strategy is evolutionarily stable.
- c. Test to see whether the long-beak strategy is evolutionarily stable.

2. Moths have always been a source of prey for many different animals. For this problem, we are going to use bears as the predator for moths. Fitness of moths are determined by how long they can live and survive from their predators. Over generations, moths have developed a darker body color to hide from their predators. In this case, moths are interacting with each other as two possible food choices for the bear. The moth that last longer will have a higher fitness level than the one that is eaten. Bears will eat the peppered moth more often because it is easier to spot. Below are some components of the evolutionary game:

- Peppered vs. peppered = (5,5)
- Peppered vs. dark = (2,8)
- Dark vs. peppered = (8,2)
- Dark vs. dark = (10,10)

- a. **Draw a game matrix for this game.**
- b. **Test to see whether the peppered strategy is evolutionarily stable.**
- c. **Test to see whether the dark strategy is evolutionarily stable.**



### Practice Problem Solutions

1. m-stability and  $\delta$ -stability
2. No they will not, the invading species will occupy the empty niche and all species in that community will be at ESS; the community is no longer invaluable by alternative strategies from within the same g-function.
3. the invasion window and invasion potential
4. *Strategies are not chosen by the organism, rather it is chosen for them as it is genetically hardwired into their systems.*  
*Many behaviors involve the interaction of multiple organisms in a population and the success if any one of these organisms depend on how its behavior interact with that of others.*

5. A.

		Hummingbird #2	
		Short	Long
Hummingbird #1	Short	2,2	1,5
	Long	5,1	4,4

B.  $p(\text{short-beak}) = 1-x$  for P1

Expected payoff for a short-beaked hummingbird with random population interactions:

- Prob.  $(1-x)$  it meets a short beaked hummingbird (S,S)  $\rightarrow u_1(S,S) = 2$
- Prob.  $(x)$  it meets a long beaked hummingbird (S,L)  $\rightarrow u_1(S,L) = 1$ 
  - $2(1-x) + 1(x) = \underline{2-x}$

Expected payoff for a long-beaked hummingbird with random population interactions:

- Prob.  $(1-x)$  it meets a short beaked hummingbird (L,S)  $\rightarrow u_1(L,S) = 5$
- Prob.  $(x)$  it meets a long beaked hummingbird (L,L)  $\rightarrow u_1(L,L) = 4$ 
  - $5(1-x) + 4(x) = \underline{5-x}$

*When  $p(\text{short})=1-x$ , expected payoff for long  $(5-x) >$  expected payoff for short  $(2-x)$  at all values for  $X$  so **short is not an evolutionarily stable strategy.***

C.  $p(\text{long-beak}) = 1-x$  for P1

Expected payoff for a short-beaked hummingbird with random population interactions:

- Prob.  $(x)$  it meets a short beaked hummingbird (S,S)  $\rightarrow u_1(S,S) = 2$
- Prob.  $(1-x)$  it meets a long beaked hummingbird (S,L)  $\rightarrow u_1(S,L) = 1$ 
  - $2(x) + 1(1-x) = \underline{1+x}$

Expected payoff for a long-beaked hummingbird with random population interactions:

- Prob.  $(x)$  it meets a short beaked hummingbird (L,S)  $\rightarrow u_1(L,S) = 5$
- Prob.  $(1-x)$  it meets a long beaked hummingbird (L,L)  $\rightarrow u_1(L,L) = 4$ 
  - $5(x) + 4(1-x) = \underline{4+x}$

*When  $p(\text{long})=1-x$ , expected payoff for long  $(4+x) >$  expected payoff for short  $(1+x)$  at all values for  $X$  so **long is an evolutionarily stable strategy.***

6. A.

		Moth #2	
		Peppered	Dark
Moth #1	Peppered	5,5	2,8
	Dark	8,2	10,10

B.  $p(\text{peppered}) = 1-x$  for P1

Expected payoff for a peppered moth with random population interactions:

- Prob.  $(1-x)$  it meets a peppered moth (P,P)  $\rightarrow u_1(\text{P,P}) = 5$
- Prob.  $(x)$  it meets a dark moth (P,D)  $\rightarrow u_1(\text{P,D}) = 2$ 
  - $5(1-x) + 2(x) = \underline{5-3x}$

Expected payoff for a dark moth with random population interactions:

- Prob.  $(1-x)$  it meets a peppered moth (D,P)  $\rightarrow u_1(\text{D,P}) = 8$
- Prob.  $(x)$  it meets a dark moth (D,D)  $\rightarrow u_1(\text{D,D}) = 10$ 
  - $8(1-x) + 10(x) = \underline{8+2x}$

When  $p(\text{peppered}) = 1-x$ , expected payoff for dark  $(8+2x) >$  expected payoff for peppered  $(5-3x)$  at all values for  $X$  so **peppered is not an evolutionarily stable strategy.**

C.  $p(\text{dark}) = 1-x$  for P1

Expected payoff for a peppered moth with random population interactions:

- Prob.  $(x)$  it meets a peppered moth (P,P)  $\rightarrow u_1(\text{P,P}) = 5$
- Prob.  $(1-x)$  it meets a dark moth (P,D)  $\rightarrow u_1(\text{P,D}) = 2$ 
  - $2(x) + 5(1-x) = \underline{1+x}$

Expected payoff for a dark moth with random population interactions:

- Prob.  $(x)$  it meets a peppered moth (D,P)  $\rightarrow u_1(\text{D,P}) = 8$
- Prob.  $(1-x)$  it meets a dark moth (D,D)  $\rightarrow u_1(\text{D,D}) = 10$ 
  - $8(x) + 10(1-x) = \underline{10-2x}$

When  $p(\text{long}) = 1-x$ , expected payoff for dark  $(10-2x) >$  expected payoff for peppered  $(1+x)$  at most values for  $X$  so **dark is an evolutionarily stable strategy.**

**Remember... a strategy is evolutionarily stable as long as the expected payoff for that strategy is greater than the other strategy at most values of  $X$ .**

A