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In a plant-pollinator system, plants have a multitude of potential signals, both visual and olfactory. Some signals are a by-product of pollen and nectar, while other can be positively correlated through pollinator conditioning. Successful pollinators are those able to cross reference signals with prior experiences to determine the integrity of their sender. An honest signal is defined as a signal correlated with an underlying characteristic; in this study: rewards. We examine honest signaling a system where high-yield and low-yield plants compete for visitation of pollinators. We model the scenario as a repeated Sir Philips Sidney game and conclude that honest signaling, in which only high yield plants signal, cannot be a Nash equilibrium because pollinators lose potential resources if they choose to skip over plants during their foraging flights.

DEVELOPMENT OF HONESTY IN REPEATED SIGNALING GAMES

by

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To my family, for their unending love and support. To the legion of educators, whose efforts have lead us here.

APPROVAL PAGE

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CHAPTER I

GAME THEORY PRELIMINARIES

1.1 Introduction

Game theory can be thought of as an analytic tool kit, assisting in the understanding the of interaction between decision making entities [OR94]. The underlying assumptions include: all *players* (decision-makers) pursue well-defined exogenous objectives (they are rational) and take into account their expectations of other players' decisions and behaviors (they reason strategically) [OR94]. The games studied can take multiple forms: non-cooperative vs cooperative, sequential games or single round, and perfect vs imperfect information. One of the strengths of game theory comes from the abstractness of its models; allowing them to be used in the study of various disciplines; from mating games in evoltionary Biology, to games modeling disease growth in Epidemolgy, to bargaining in Economics. [BR13].

1.2 What is a Game?

A *game* is a mathematical description of an interaction between two or more players that prescribes set of actions that each player can take and incentives to each player [BR13]. While games are useful in studying the consequences/rewards that follow from various decisions, they do not inherently tell us what actions player do or should take. Formally:

Definition 1.1. A **Game** consist of a *set of players*, N, for each player i there is a *strategy set*, A_i, from which they select their actions, and for each *outcome* (or strategy combination) of the game there is a *payoff* for each player.

Let a, $b \in A_1 \times A_2 \times ... \times A_n$ be two strategy combinations, that is:

$$a = \begin{bmatrix} a_1, & a_2, & ..., & a_i, & ..., & a_n \end{bmatrix}, b = \begin{bmatrix} b_1, & b_2, & ..., & b_i, & ..., & b_n \end{bmatrix} \tag{1.1}$$

where a_i, b_i are the actions chosen by player i, and n is the total number of players ($n = |N|$). The function $u_i : A_1 \times A_2 \times ... \times A_n \to \mathbb{R}$, is the *utility* ,or *payoff*, function for player i.

We further define a game with a finite number of players, and a finite number of actions for each player, as a game in *normal form.* A natural representation of these games is via an n-dimensional matrix. The matrix representation of these games are called *payoff matrices*; where the payoff for player i, in the strategy combination $S = \begin{bmatrix} s_{a_1}, s_{a_2}, ..., s_{a_n} \end{bmatrix}$, is the i-th component of the $a_1, a_2, ..., a_n$ entry of the matrix.

Example 1.2. A classic example of decision making can be found in a game of *Rock-Paper-Scissor (R-P-S).* Two players are placed in the situation of simultaneously choosing between one of three strategies "Rock", "Scissor", or "Paper". Players gain or lose points based on the conventions "Rock beats Scissor", "Scissor beats Paper", and "Paper beats Rock". The results of such an engagement can be represented by the following payoff matrix:

$$\begin{array}{cc} & \text{Player 2} \\ & \begin{array}{ccc} R & P & S \end{array} \\ \text{Player 1} \quad \begin{array}{c} R \\ P \\ S \end{array} & \begin{pmatrix} (0,0) & (-1,1) & (1,-1) \\ (1,-1) & (0,0) & (-1,1) \\ (-1,1) & (1,-1) & (0,0) \end{pmatrix} \end{array}$$

where the first entry in each pair represents the payoff for Player 1 and the second entry the payoff of Player 2.

In Example 1.2, the strategy of playing Rock can be expressed as $\begin{bmatrix} 1 & 0 & 0 \end{bmatrix}$. Using standard matrix multiplication we can compute the payoffs for any combination of actions, called the *expected payoff*; for actions p, q,the expected payoff is denoted $\mathscr{E}[p, q]$. For a matrix game, $\mathscr{E}[p, q] = pAq^T$, where A is the payoff matrix for the game. Thus, in R-P-S, the expected payoff for the actions of Rock vs Paper (Player 1 and Player 2 respectively) is

$$\begin{bmatrix} 1 & 0 & 0 \end{bmatrix} \begin{bmatrix} (0,0) & (-1,1) & (1,-1) \\ (1,-1) & (0,0) & (-1,1) \\ (-1,1) & (1,-1) & (0,0) \end{bmatrix} \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix} = \tag{1.2}$$

$$\begin{bmatrix} (0,0) & (-1,1) & (1,-1) \end{bmatrix} \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix} = (-1,1). \tag{1.3}$$

The result of $(-1, 1)$ denotes that Player 1 lost one point and Player 2 gained one point.

1.2.1 Strategies

In the Example 1.2, the actions described represented *pure strategies.* That is a player using $\begin{bmatrix} 1 & 0 & 0 \end{bmatrix}$ will play Rock with a 100% certainty. The number of pure strategies available to Player i is denoted $k(i) = |A_i|$ However, these are not the only types of strategies available to players.

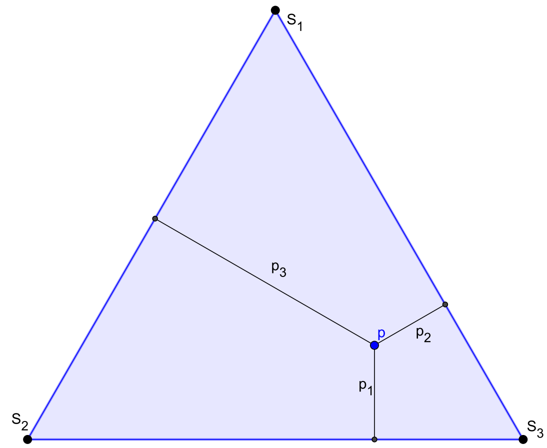

Figure 1. Strategy Simplex with Mixed Strategy p Adopted from [BR13].

For example, Player 1 may decide he would like to pick Paper or Scissor with equal probability (chosen by a fictitious coin toss), this strategy could also be represented in a matrix game as $\begin{bmatrix} 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix}$. These strategies which do not conform to a single pure strategy are called *mixed strategies*. In particular, a mixed strategy, p, for Player i is a probability distribution on the set A_i, such that, $\sum_{j=1}^{k(i)} p_j = 1$, where p_j is the probability of pure strategy a_j being played.

Definition 1.3. The **support** of a mixed strategy p, denoted $\mathscr{S}(p)$, is the set of indices for which pure strategy i has a non-zero chance of being played. That is

$$\mathscr{S}(p) = \{j : p_j > 0\}.$$

We can describe the space of all strategies (mixed and pure) of a normal form game, with n pure strategies, by the interior of an $(n-1)$-dimensional unit simplex. A *simplex* is a generalization of an equilateral triangle to arbitrary dimensions. For $\mathbb{R}^2$ we have an equilateral triangle (see Figure 1), $\mathbb{R}^3$ a tetrahedron, and $\mathbb{R}^4$ a 5-cell. In Figure 1, we can see mixed strategy $p = \begin{bmatrix} p_1, & p_2, & p_3 \end{bmatrix}$

represented as a point p with minimum distances p_1, p_2, p_3 from the sides opposite vertexes S_1, S_2, S_3 respectively. An advantage to this representation is that we can describe the set of mixed strategies as a close, convex, compact subset of $\mathbb{R}^n$. In particular as in [BR13], we can describe mixed strategy p as

$$p = \begin{bmatrix} p_1, & p_2, & p_3, & ... \end{bmatrix}$$

Motivated by this representation, we call a mixed strategy p an *internal strategy* if every pure strategy has a non-zero chance of being played.

1.2.2 Solving a Game

So far, we've established representations for modeling the interactions between individuals, but have yet to specify a method of "solving" a game. Motivated by the variations that can occur in a player's payoff depending upon the actions of others (i.e. for two strategy combinations a and b ,$u_i(a) \geq u_i(b)$, regardless of whether Player i has changed their move) we define the *best response* of Player i, against the given actions of the other players.

Definition 1.4. Let S be a strategy played by Player i and T^{*_i} be a strategy combination with the i^{th} entry removed; that is T^{*_i} is the combination of the actions taken by all other players except Player i: T^{*_i}.

$$T^{*_i} = \begin{bmatrix} a_1, & a_2, & \ldots & a_{i-1}, & a_{i+1}, \ldots, & a_n \end{bmatrix}.$$

We call a strategy S Player i's **best response** to strategy combination T^{*_i} if

$$\mathscr{E}_i[S', T^{*_i}] < \mathscr{E}_i[S, T^{*_i}], \text{ for all other startegies } S' \text{ in } A_i,$$

where $\mathscr{E}_i[S, T^{*_i}]$ denotes the expected payoff for Player i using S against T^{*_i}. In other words S is Player i's best response to T^{*_i} if he achieves a higher payoff by playing strategy S against T^{*_i} than he would if he played any other strategy S' available to him.

Example 1.5. In R-P-S, Player 1's best response against Player 2 playing "Rock" is to play "Paper", as :

$$1 = \mathscr{E}_1[P, R] > 0 = \mathscr{E}_1[R, R] > -1 = \mathscr{E}_1[S, R]. \tag{1.4}$$

Example 1.6. We illustrate the concept of best response with the brief analysis of the *Hawk-Dove Game*. In this game, two animals are fighting over a resource, perhaps a piece of food. Both animal can choose between two behaviors,: an aggressive hawkish behavior H, or an accommodating dovish behavior, D. The total resource is worth 4 to each of them. When a hawk meets a dove, it gets all of the resource without the need to fight. When two doves meet they split the prize evenly.

When two hawks meet, due to the aggression of the interaction, each player incurs a cost of (-4) in the course of fighting, before splitting the prize evenly. Shown as:

$$A = \begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} (-2,-2) & (4,0) \\ (0,4) & (2,2) \end{pmatrix}. \end{array}$$

If Player 2 were to play strategy H, the Player 1's best response would be to play strategy D as $0 > -2$; however if Player 2 was to play strategy D, then Player 1's best response would be to play strategy H, as $4 > 2$, instead [LBS08].

Even with the concept of best response, a solution has yet to be realized; in a normal form game, Player 1 may not know exactly what Player 2 will do. As in Example 1.6, Player 1's best response may change depending on which strategy Player 2 is playing. What we would like to find is a stable state for this game. In such a state, if reached, no player would benefit from switching their strategy; and thus a further rounds of the game would replicate those decisions. This is the motivation behind a *Nash equilibrium.*

A Nash equilibrium is an outcome of a game in which no player can profit from any unilaterally deviation of their strategy. In terms of a best response, the strategies each player implements must be their best response to all other players' actions. Otherwise, at least one Player i(would prefer to change their strategy, in order to achieve a higher payoff.

Definition 1.7. For an n-player game, we say that strategy combination

$$a^* = \left[a_1^*, a_2^*, ...a_i^*, ..., a_n^*\right]$$ is a **Nash equilibrium** if for all player's i

$$\mathscr{E}_i(a^*) \geq \mathscr{E}_i(a)$$

for all $a = \left[a_1^*, a_2^*, ..., a_i', ..., a_n^*\right]$ with $a_i^* \neq a_i'$ and $\mathscr{E}_i$ is the expected payoff for Player i [OR94].

In a two player game, we say $[p^*, q^*]$ is a **strict Nash equilibrium** if :

$$\mathscr{E}_1[p^*, q^*] > \mathscr{E}_1[p, q^*], \text{ for all } p \neq p^* \tag{1.5}$$

$$\mathscr{E}_2[q^*, p^*] > \mathscr{E}_2[q, p^*]. \text{ for all } q \neq q^*. \tag{1.6}$$

And $[p^*, q^*]$ is a **weak Nash equilibrium** if:

$$\mathscr{E}_1[p^*, q^*] \geq \mathscr{E}_1[p, q^*], \text{ for all } p \neq p^* \tag{1.7}$$

$$\mathscr{E}_2[q^*, p^*] \geq \mathscr{E}_2[q, p^*]. \text{ for all } q \neq q^*. \tag{1.8}$$

1.3 Games in Extensive Form

A game in *extensive form*, also called a *sequential game*, is a game governed by a sequence of moves, where each action is decided upon by one of the players of the game, or by chance [BR13]. With these games, player may no longer be required to simultaneously make their decision, but do so in multiple stages [AC00]. Sequential games are closely tied with a graph representation, called a *game tree*.

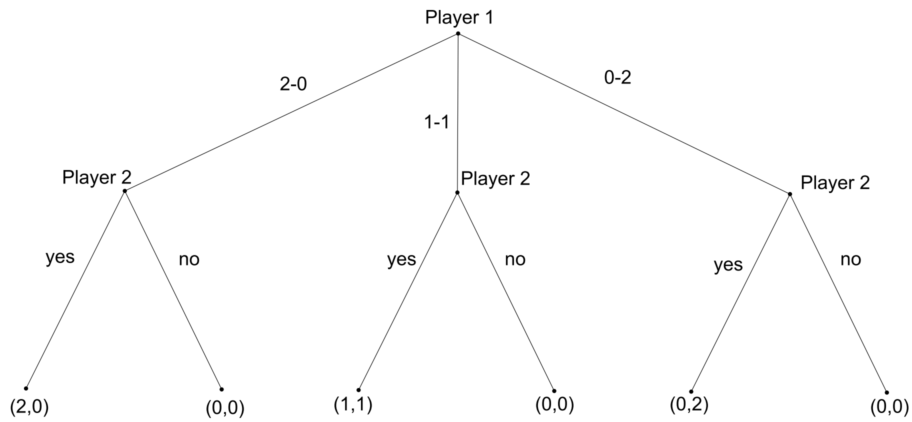

Figure 2. Sharing Game Tree. Here, $(2,0)$ means that after Player 1 played $2-0$ and Player 2 played *yes*, Player 1 receives payoff of 2 and Player 2 receives payoff of 0. Similarly for other entries.

Definition 1.8. A tree (which is a simple directed, connected graph which contains no cycles) is said to be an n-person **game tree** if

(a) each non-terminal node of the tree is "owned" by exactly one player, and

(b) at each terminal node, v, of the tree has an n-dimensional "payoff" vector

$$p(v) = \left[p_1(v), \quad p_2(v), \quad ..., \quad p_n(v)\right],$$

where the $p_i(v)$ represent the payoff for player i at vertex v, is assigned [AC00].

Each non-terminal node is called a *decision node*; during the course of a game, the player who "owns" a decision node makes an action if that node is reached. Actions in game trees are signified by edges of the graph. It is possible, in an sequential game, for a player to not own any nodes at all. Figure 2 the game tree for the *sharing game*.

1.3.1 Extensive Form with Perfect Information

With the introduction of sequential consequences, the ideas of *histories* and *available actions* must be discussed. For now a history can be intuitively thought of as a recollection of some, but not necessarily all, previous actions of the game and available actions are the notion that, depending on what has transpired in the game, a player's actions might differ from turn to turn. Some common examples of extensive form games can be found in the conventional games of chess, checkers, and poker, others in the realm of free market economies with games of price war and auctions. In each of these games, the actions players take can be seen to follow in sequence.

Before defining a sequential game, we first introduce the concept of *information partitions.*

Definition 1.9. In a game tree, the set of nodes $\mathcal{I}_j = \{N_1, N_2, ..., N_L\}$ is called an **information partition**, or **information set**, for Player j if:

(a) all nodes in $\mathcal{I}_j$ are non-terminal and belong to Player j

(b) if N_x and N_y are members of $\mathcal{I}_j$ then N_x and N_y are not related; i.e. N_x is neither a successor nor an ancestor of N_y; that is N_x comes neither directly before, nor directly after N_y.

(c) all nodes in $\mathcal{I}_j$ are equivalent; that is for all N_x and N_y in $\mathcal{I}_j$, N_x and N_y have the same number of edges starting from them, and the set of edges starting from N_x is "identical" to the set of edges starting from N_y.

[AC00]

The intuition behind these information partitions comes from the idea of uncertainty. Two nodes are in the same information partition of Player j if he cannot discern, due to some lack of information, which node he is at. For example in a two player game of texas hold'em, Player 2 does not know what cards Player 1 has, however he is fully aware of what cards he holds himself. When make the decision of how much to bet, his cards are the only information Player 2 has. An information partition in this game is the set of all nodes in which Player 2 holds those exact same cards, while all Player 1's cards are the various two card combination which Player 1 could start with.

Definition 1.10. A **sequential game**, or **game in extensive form**, is an n-player game tree such that the decision nodes are partitioned into information sets that belong to the players [AC00].

We further define a sequential game with *perfect information* as a sequential game in which the information sets of Player j, for all Players in the game, contain only one node each. In other words, all players know exactly what node he or she is making a decision at, during all points of the game. Chess or checkers are example of these types of games.

In sequential games, there is a notion of prior actions, a list of which is captured in the notion of *histories*. Histories are vectors which account prior actions taken in a game. As the game progresses, these vectors my update to reflect the actions taken. In games with perfect information, each player is capable of complete recollection.

Example 1.11. [LBS08] Imagine a brother and sister are sharing two indivisible presents from their parents. The brother suggest a potential distribution of the gifts: either he keeps both (2-0), they split fairly (1-1), or she gets both (0-2). The sister then can accept the offer or decline. If she agrees then the presents are distributed as prescribed, if she does not then neither receives any gifts; resulting in a payoff of 0 for both of them. The set of actions, A_i available to each player are as follows; the brother is Player 1 and the sister is Player 2,

- $A_1 = \{(2-0), (1-1), (0-2)\}$, $|S_1| = 3$
- $A_2 = \{(yes, yes, yes), (yes, yes, no), (yes, no, yes), (no, yes, yes),$
  $(yes, no, no), (no, yes, no), (no, no, yes), (no, no, no)\}$, $|S_2| = 2^3$

Before the game is played, the sister does not know what her brother may do. Therefore the strategies available to the sister are the decisions she is willing to make given any possible action of her brother. The strategy (yes, no, yes) means that she will agree to either her brother or her getting both gifts, but will disagree to splitting them. Figure 2 is the game tree representation of this game.

1.3.2 Finding Solutions

A natural question that arises is how does one begin to find, say, a Nash equilibrium for an extensive form game? To begin, we first define a *subgame* of game G.

Definition 1.12. Given an extensive form game G, the **subgame** of G rooted at node h is the restriction of the tree of G to the successors of h [LBS08].

In Example 1.11 the subgame formed from the node following the "1-1" edge, and the nodes that below it. This subgame can be solved by Player 2 simply choosing which ever option yields the greatest payoff. More generally, at any terminal vertex, the prior acting player will benefit most by choosing their best response to the current history. When the entire game is considered, with perfect information, any extensive form game can be solved by an application of this logic, called *subgame perfect equilibrium.*

Definition 1.13. A **subgame perfect equilibrium of an extensive form game** is a set of strategies which produce a Nash equilibrium. More specifically, it is a set of strategies in which no player can unilaterally benefit from changing any of their actions.

By definition, a subgame perfect equilibrium is also a Nash equilibrium. A convenient method of finding these subgame perfect equilibrium is *backwards induction.* The basic idea of backwards induction involves examining the "bottom-most" subgames, identify equilibrium in those, and then work back up and consider increasingly larger tree [OR94]. Since this is a game with perfect information, each player is rationally able to identify their best responses in any given scenario.

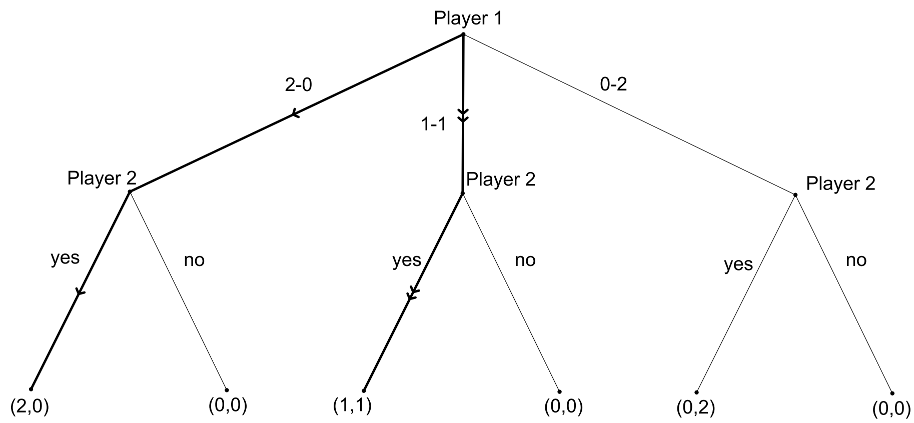

Figure 3. Solution to Sharing Game. Subgame perfect equilibrium to example 1.14.

Example 1.14. From Example 1.11, the game tree in Figure 2 was constructed. We will solve this game using backwards induction. Starting from the bottom subtree of the "$0-2$" route. For Player 2, the action of "yes" strictly dominates the action of "no" as $2 > 0$. In the subtree of the "$1-1$" route, the action of "yes", again, strictly dominates the action "no" as $1 > 0$. In the subtree of "$2-0$", Player 2 is indifferent in her decision, as $0 = 0$; she may threaten the action of "no", as it would reduce Player 1's payoff, but this is not a credible threat (i.e. she has no incentive built in for it). Now Player 1 rationalizes all these scenarios and is now able to make his first action based on the potential payoff he receives, should those scenarios be carried out by Player 2. There are two subgame perfect equilibria to this game: $(2-0, yyy)$and $(1-1, nyy)$. This result can be seen in Figure 3.

1.3.3 Extensive Form with Imperfect Information

We now extend our definition of an extensive form game to one in which not all players are fully informed about various positions of the game. In particular, *extensive games with imperfect information* focus on games in which players may not be informed as to some (or all) the actions that have all ready occurred. A natural extension of definition 1.10 follows.

Definition 1.15. A sequential, or game in extensive form, with **imperfect information** is any sequential game which does not have perfect information.

The game tree of a sequential game with imperfect information denotes the nodes within the same information by connecting them with dashed lines. In Figure 4, all nodes available to Player 2 are within the same information set. A consequence that follows from these information partitions is that backwards induction may no longer be possible. If two nodes are in the same information set, then the player who owns them cannot distinguish what results may follow. In Figure 4, it can be seen that Player 2's best response cannot be determined, as at each node he does not know what outcome may follow.

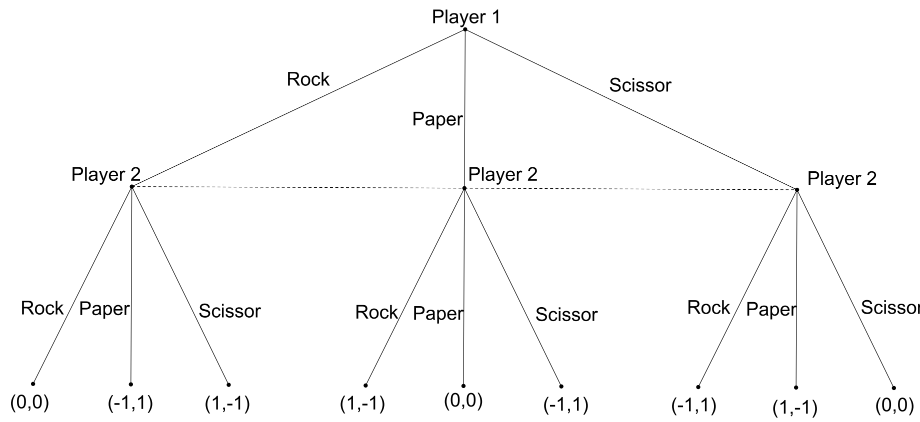

Figure 4. Extensive Game with Imperfect Information. Game of R-P-S.

Example 1.16. In Figure 4, the dashed line denotes that at that node, the acting player does not have information to previous actions. All histories for Player 2 are in the same information partition. At each, he/she knows that Player 1 has picked a move (though they do not know what action) and now they must chose one for them self.

In some extensive form games with imperfect information, an indifferent randomizer agent, "Nature", is included with the set of players. When a node is owned by Nature, the action chosen is decided by some probability distribution on the set of available actions. An example of this can be found in the dealer in a game of poker. The actions of the dealer are non-bias and random based on the composition of the deck of cards.

CHAPTER II

BIOLOGY

Apis mellifera, the honeybee, is a prime example of the advantages of cooperation and organization. These social insects live and work together, without the need of an central organizer, to create a functional unit whose abilities transcend those of the individuals [See10]. As a human body is sustained through the fuctions of various cells, so too is a hive sustained by the efforts of its denizens. Though it is easy for one to think of a single bee an organism, a fuller understanding of the honey bees' potential comes from viewing the hive as a thoroughly integrated unit [See09].

A colony is composed of three types of individuals: a relatively small population of drones- males whose primary purpose is reproduction, an overwhelming majority of workers- females which fill a wide array of roles, and a single queen- a larger female whose sole purpose is to mate and lay eggs. The workers execute the vast majority of tasks for the hive. Workers regulate the internal temperature of the hive. During cold winter months heat-producing bees are allocated to central brood rearing area of the hive [See10]; increased clustering has also been observed. During the summer workers increase water collection and allow evaporation to cool the hive. Workers determine when a queen in getting too old to serve the colony by monitoring her pheromone levels and egg laying abilities; they note when it is time to raise new queens. They build the hive, constructing and repairing its various combs, and during swarms they ultimately choose the location of the new hive. Of course, they are also the foragers who set out and retrieve the pollen and nectar stores to sustain the hive.

On average, the hive must meet a yearly quota of 20 kg of pollen and 120 kg of nectar in order to ensure survival during the winter months [See09]. It must achieve this while also supplying the colony with its daily nutrition. Coordinating an effective foraging operation assist in achieving these quotas. Hives have been seen to forage in areas larger than 100 km^2 [See09]. The scope of this achievement can be recognized when one considers the size of these gatherers. Honey bees must locate high yield plants shortly after they bloom, else risk losing them to neighboring colonies. Once located, foragers return to the hive and communicate the location, relative to the sun, of these resources by use of the *waggle* or *recruitment dance*. This means of communication is also utilized when determining the location of new hives.

Honey bees have shown the ability to be selective among their potential food sources. The recruitment dance provides the hive with an avenue of coordinating foraging patterns. This process has been observed to be reactive to daily changes in food sources. Foraging patterns can be completely altered in as little as four hours [**?**]. Natural causes of resource changes can be caused by varying amounts of sunlight or soil moisture, but can also be due to increased competition between other pollinators. The threshold for what is considered a resource worth visiting to can be raised or lowered depending on the needs of the hive.

In addition to selecting among their available resources, honey bees are able to identify signals which are associated with high quality of resources [KS15]. *Phenylactaldehyde* is an olfactory compound correlated with high quality nectar;

while it may be hypothesized that honey bees rely heavily on this scent, honeybees have been observed to forgo this signal, developing preference for others signals, if it deemed dishonest [KS15].

It is well known that flowers exhibit various signals in order to attract visitation from pollinators. An honest signal can be thought of as one which reliably reflects the underlying qualities of the signaler [DG91]. Patterns of pigmentation, such as those displayed by the common snapdragon [WMR+13], directly correlated to high quality nectar, as an example. Dishonest signaling, those that do not reflect quality, also exist. *Ophrys apifera*, the bee orchid, emits a scent that mimics female a female bee during mating season; as a result, male bees, attempting to copulate, visit and inadvertently pollinate the orchids [Dod76]. Dishonest signals are often produced by individuals who lack some characteristics to prosper in their systems normally. Many conventional signaling systems, due to the energy cost associated with the receiver probing the signalers, are susceptible to cheating.

CHAPTER III

REPEATED SIR PHILIPS SIDNEY GAME

3.1 Biological Question

In a signaling game, both players are capable of manipulating the information available to the each other. In a plant-pollinator system, plants are able to advertise the quantity/quality of their nectar (or other reward) through various visual or olfactory signals. The pollinator is able to decide its general response to these signals. If a signal leads a pollinator to a high quality reward, then the pollinator will learn to respond to the signal with greater frequency. If an abundance of false, or dishonest, signals are conveyed, then the pollinator will eventually ignore the signal all together; by decreasing the probability of visiting plants using that signal. Pollinators can be conditioned to learn the correlation between a signal and rewards.

We search for the parameters, defined in Table 1, which encourage honest signaling to be evolutionarily stable. In the plant-pollinator system, we define honest signaling as the signaling tendency where high yield plants signal and low yield do not.

Pl_H	High yielding plant
Pl_L	Low yielding plant
Pol	Pollinator
	Parameters
α	High yield proportion of plant population $(1 \geq \alpha \geq 0)$
N_B	Number of pollinators that would potentially visit a flowering plant
C_L	Cost for low yielding plant to signal$(C_L < 1)$
C_H	Cost for high yielding plant to signal$(C_H < C_L < 1)$
V_H	Reward for pollinator visiting a high yield plant $(V_H > 0)$
V_L	Reward for pollinator visiting a low yield plant $(V_H > V_L > 0)$
R	Number of rounds the pollinator can visit a plant
ω_S	Probability for a pollinator to visit a signaling plant
ω_N	Probability for a pollinator to visit a non-signaling plant
t	Number of rounds a pollinator can retain information
	Strategies
S	Plant of a given type will signal
N	Plant of a given type will not signal
XY	Pl_H, Pl_L will perform strategies X,Y respectively. $X, Y \in \{S, N\}$
P_{S_L}	Probability deducted from ω_S per low yield signaling plant in last t rounds$(P_{S_L} \leq 1)$
P_{N_0}	Initial probability for pollinator to visit a non-signaling plant$(P_{N_0} \leq 1)$
P_{N_H}	Probability added to ω_N per high yield non-signaling plant in last t rounds$(P_{N_H} \leq 1 - P_{N_0})$

Table 1. Table of Notation

3.2 The Mathematical Model

Let α be the proportion of high yield plants in the environment and $1-\alpha$ be the proportion of low yield plants. Initially, the pollinator does not know whether a plant it is considering is high or low yield. The plant can take the action to signal to the pollinator, which incurs a cost on the plant C_H or C_L,; where C_H is the cost for a high yield plant to signal and C_L is the cost for a low yield plant to mimic that signal.

The pollinator then decides to visit the plant or not based on the probability of visiting a signaling plant, ω_S, or the probability of visiting a non-signaling plant, ω_N. These probabilities are determined based on the results of previous encounters experienced by the pollinator. If the pollinator decides to visit the plant, it receives a payoff of V_H or V_L, depending on whether a high yield or low yield plant was visited respectively. The visited plant receives a payoff of 1. Figure 5 is the game tree representation of a single round of the game.

If the game is played a single time, it does not benefit the pollinator to ever skip a plant because the reward is always positive ($V_H > V_L > 0$). By transitioning to a finitely repeated game, in which the pollinator is allowed to visit R plants, the pollinator can benefit in the long term by skipping a plant in order to condition the plant population's signaling tendencies. The pollinator develops the behavior to skip some plants, based on the plants' actions, and visit others; despite the fact that the pollinator will get less reward in the singular round than in it would otherwise. For the plants, the repeated game provides multiple opportunities to be visited by a potential pollinator, thus the chance of being visited for both signaling and not signaling are available.

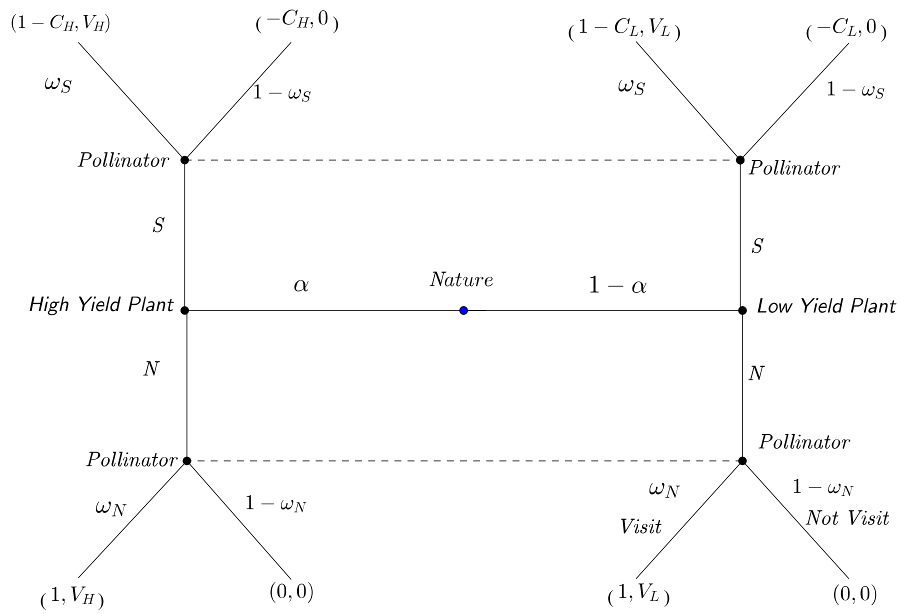

Figure 5. Plant-Pollinator Extensive Form Game. A pollinator arrives at a high yield or low yield plant, with probability α or $1-\alpha$ respectively, depending on the proportion of high yield and low yield plants in the population respectively. The plant is either signaling (S) or not signaling (N). The pollinator then visits the plant with probability ω_S or ω_N; depending whether the plant is signaling or not.

3.3 Updating ω_S and ω_N

In any particular round, the pollinator must decide whether or not to visit a plant which is signaling or non-signaling. The pollinator references the outcomes of the previous rounds by means of two history vectors: $\mathcal{H}_S$ and $\mathcal{H}_N$, which contain the information of the outcomes of the previous t signaling flowers visited and the previous t non-signaling flowers visited, respectively. Depending upon their entries, a pollinator may visit or skip a plant accordingly.

At the beginning of the game, $\mathcal{H}_S$ and $\mathcal{H}_N$ are both empty. After a pollinator visits a plant, it is able to assess its reward, and categorizes the plant as a high yield or low yield. Bases on this assessment, if the plant was a low yield plant and was signaling, then $\mathcal{H}_S$ is updated by the concatenating $\mathcal{H}_S \frown [L]$; denoting that a signaling low yield plant was visited. If $\mathcal{H}_S$ already has t entries, then the first entry is is discarded $((\mathcal{H}_S) \mapsto (\mathcal{H}_S)^{*1})$, all remaining entries are index down by one $((\mathcal{H}_S)_{i,1} \mapsto (\mathcal{H}_S)_{i-1,1})$, then concatenation occurs normally. Updating $\mathcal{H}_N$ is conducted likewise. It is from these history vectors that the pollinator calculates ω_S and ω_N.

The general form of ω_S and ω_N are as follows:

$$\omega_S = 1 - \frac{K_L}{t} P_{S_L} \tag{3.1}$$

$$\omega_N = P_{N_0} + \frac{K_H}{t} P_{N_H}. \tag{3.2}$$

K_L represents the number of signaling low yield plants visited in the last t signaling plants visited (the number of L's in $\mathcal{H}_S$); and K_H is the number of non-signaling high yield plants visited in the last t non-signaling plants (the number of H's in $\mathcal{H}_N$). P_{N_0}, P_{N_H}, and $pslm$ are as defined in Table 1.

3.4 Calculating Average ω_S and ω_N

A plant strategy XY is a strategy in which high yield plants play strategy X and low yield plant play strategy Y; X and Y, can take the the values of S or N. For each combination of plant strategies, an average ω_S and ω_N can be calculated.

As the strategies that high and low yield plants vary, so too does the values of K_L and K_H. Particularly, the expected values of K_L and K_H take the following values

$$E[K_L] = \begin{cases} (1-\alpha)t & SS, \\ t & NS, \\ 0 & else. \end{cases} \tag{3.3}$$

$$E[K_H] = \begin{cases} \alpha t & NN, \\ t & NS, \\ 0 & else \end{cases} . \tag{3.4}$$

3.4.1 *Average Value of ω_S and ω_N in SS Plant Population*

With all plants signaling, we examine the general formula for ω_S. As both plants are signaling, $K_L \sim Binomial((1-\alpha), t)$, and $K_H = 0$.

$$E[\omega_S] = 1 - \frac{E[K_L]}{t} P_{S_L} = 1 - \frac{(1-\alpha)t}{t} P_{S_L} = 1 - (1-\alpha)P_{S_L}. \tag{3.5}$$

Since high yield plants are signaling ω_N has no chance to improve. By equation 3.4

$$E[\omega_S] = P_{N_0} + \frac{E[K_H]}{t} P_{N_H} = P_{N_0} + 0 = P_{N_0}. \tag{3.6}$$

3.4.2 Average Value of ω_S and ω_N in SN Plant Population

Since no low yield plant will be signaling, so $K_L = 0$, ω_N will never be penalized and thus

$$E[\omega_S] = 1 - \frac{E[K_L]}{t} P_{S_L} = 1 - 0 = 1. \tag{3.7}$$

Similar to the previous case, as all high yield plants are signaling, $K_H = 0$, and ω_N will never grow and

$$E[\omega_N] = P_{N_0} + \frac{E[K_H]}{t} P_{N_H} = P_{N_0} + 0 = P_{N_0}. \tag{3.8}$$

3.4.3 Average Value of ω_S and ω_N in NS Plant Population

Since only low yield plants will be signaling, ω_S will always be penalized. By equation (3.3),

$$E[\omega_S] = 1 - \frac{E[K_L]}{t} P_{S_L} = 1 - P_{S_L}. \tag{3.9}$$

Since low yield plants are signaling and high yield are not, $K_H = t$, ω_N achieves maximum benefit and

$$E[\omega_N] = P_{N_0} + \frac{E[K_H]}{t} P_{N_H} = P_{N_0} + P_{N_H}. \tag{3.10}$$

3.4.4 Average value of ω_S and ω_N in NN plant population

Since no low yield plants will be signaling, ω_S will incur no penalty, $K_L = 0$

$$E[\omega_S] = 1 - \frac{E[K_L]}{t} P_{S_L} = 1 - 0 = 1. \tag{3.11}$$

As both types of plants are non-signaling, $K_H \sim Binomial(\alpha, t)$. By (3.2),

$$E[\omega_N] = P_{N_0} + \frac{E[K_H]}{t} P_{N_H} = P_{N_0} + \frac{\alpha t}{t} P_{N_H} = P_{N_0} + \alpha P_{N_H}. \tag{3.12}$$

3.5 Calculating Payoffs for Plant

3.5.1 Expected Payoff for SS

For a plant, the payoff depends on whether or not the plant is visited at all. To capture this, we will sum all the probabilities of being visited by the i^{th} pollinator and then consider the consequence of not being visited.

For a low yield plant

$$\mathscr{E}_{Pl_L}[SS] = \sum_{i=0}^{N_B - 1} \big(\substack{\text{Probability of being visited at} \\ \text{round } i+1}\big)(\text{reward-cost}) + \big(\substack{\text{Probability of} \\ \text{not being visited}}\big)(\text{cost of signaling}) \tag{3.13}$$

$$= \sum_{i=0}^{N_B - 1} (1 - E[\omega_S])^i E[\omega_S](1 - C_L) + (1 - E[\omega_S])^{N_B}(-C_L). \tag{3.14}$$

As this is a truncated geometric series, whose sum has denominator $E[\omega_S]$,

$$\mathscr{E}_{Pl_L}[SS] = (1 - E[\omega_S])^{N_B}(1 - C_L) + (1 - E[\omega_S])^{N_B}(-C_L). \tag{3.15}$$

By substituting from (3.5) for $E[\omega_S]$ for the SS case we have:

$$\mathscr{E}_{Pl_L}[SS] = (1 - ((1-\alpha)P_{S_L}))^{N_B}(1 - C_L) + (1 - (1-\alpha)P_{S_L})^{N_B}(-C_L) \tag{3.16}$$

$$= (1 - C_L) - ((1-\alpha)P_{S_L})^{N_B}. \tag{3.17}$$

By a similar derivation. The expected payoff of high yielding plant is

$$\mathscr{E}_{Pl_H}[SS] = (1 - C_H) - ((1-\alpha)P_{S_L})^{N_B}. \tag{3.18}$$

3.5.2 Expected Payoff for SN

The expected payoff for Pl_L in this case is similarly done, with the notable exception that the plant incurs not cost for not-signaling.

$$\mathscr{E}_{Pl_L}[SN] = (\underset{\text{being visited}}{\text{Sum of the probabilities of}})_{\text{(reward-cost)}} + (\underset{\text{visited at all}}{\text{Probability of not being}})_{\text{(no cost)}} \tag{3.19}$$

$$= \sum_{i=0}^{N_B - 1} (1 - E[\omega_N])^i (E[\omega_N])(1) + (1 - E[\omega_N])^{N_B}(0). \tag{3.20}$$

Similarly to the SS case, this is a truncated geometric series, whose sum's denominator is $E[\omega_N]$. Thus

$$\mathscr{E}_{Pl_L}[SN] = 1 - (1 - E[\omega_N])^{N_B}. \tag{3.21}$$

By (3.8)

$$\mathscr{E}_{Pl_L}[SN] = 1 - (1 - P_{N_0})^{N_B}. \tag{3.22}$$

For high yield plants

$$\mathscr{E}_{Pl_H}[SN] = \sum_{i=0}^{N_B-1} (1 - C_H)(E[\omega_S])(1 - E[\omega_S])^i + (1 - E[\omega_S])^{N_B}(-C_H) \tag{3.23}$$

$$= \frac{(1 - C_H)(E[\omega_S])(1 - (1 - E[\omega_S])^{N_B})}{(1 - (1 - E[\omega_S]))} \tag{3.24}$$

$$= (1 - C_H)(1 - (1 - E[\omega_S])^{N_B}). \tag{3.25}$$

By (3.7)

$$\mathscr{E}_{Pl_H}[NS] = (1 - C_H)(1 - (1 - 1)^{N_B}) = (1 - C_H). \tag{3.26}$$

3.5.3 Expected Payoff for NS

Through similar derivations, by (3.9)

$$\mathscr{E}_{Pl_L}[NS] =(1-C_L)(1-(1-E[\omega_S])^{N_B}) + (-C_L)(1-E[\omega_S])^{N_B} \tag{3.27}$$

$$=(1-C_L)(1-(1-(1-P_{S_L}))^{N_B}) + (-C_L)(1-(1-P_{S_L}))^{N_B}) \tag{3.28}$$

$$=(1-C_L)(1-(P_{S_L})^{N_B}) + (-C_L)(P_{S_L})^{N_B} \tag{3.29}$$

$$=(1-C_L)-(1-C_L)(P_{S_L})^{N_B} + (-C_L)(P_{S_L})^{N_B} \tag{3.30}$$

$$=(1-C_L)-(P_{S_L})^{N_B} + (C_L)(P_{S_L})^{N_B} + (-C_L)(P_{S_L})^{N_B}. \tag{3.31}$$

Thus,

$$\mathscr{E}_{Pl_L}[NS] = (1-C_L)-(P_S)^{N_B}. \tag{3.32}$$

For high yield

$$\mathscr{E}_{Pl_H}[NS] =(1)(1-(1-E[\omega_N])^{N_B}). \tag{3.33}$$

By (3.10)

$$\mathscr{E}_{Pl_H}[SN] = 1-(1-(P_{N_0}+P_{N_H}))^{N_B}. \tag{3.34}$$

3.5.4 Expected Payoff for NN

For this last strategy, we have a unique case were the payoff for high and low yield plants are identical. Since neither incurs a cost, their payoffs are simply due to the probability that a pollinator will visit them.

$$\mathscr{E}_{Pl_L}[NN] = 1 - (1 - P_{N_0} + \alpha P_{N_H}))^{N_B} = \mathscr{E}_{Pl_H}[NN]. \tag{3.35}$$

3.6 Calculating Payoffs for Pollinator

For the Pollinator, its payoff is determined by the number of high and low yield plants it visit over the course of R rounds. The pollinator does have the chance to skip a plant entirely with probability $1 - \omega_S$ for signaling plants, and $1 - \omega_N$ for non-signaling. The Pollinator may decide how much it punishes, through reducing the probability of visiting signaling plants, deceptive or dishonest signals P_{S_L}; namely low yield plants signaling. The pollinator chooses it's initial probability of visiting a non-signaling plant P_{N_0}, and how much it learns to "trusts" non-signaling plants when it experiences high yield plants not signaling, P_{N_H} .

3.6.1 Expected Payoff in SS Plant Population

The expected payoff of the pollinator is based on the expected payoff of a single round, multiplied R times. In a single round, the payoff for the pollinator is given by the probability of visiting a signaling plant times the reward associated, plus the probability of visiting a non-signaling plant times the reward associated. In the SS case, since both plants are signaling, the reward for visiting a non-signaling plant is 0. Thus,

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[(E[\omega_S])(\alpha V_H + (1-\alpha)V_L) + E[\omega_N](0)] \tag{3.36}$$

$$= R[(E[\omega_S])(\alpha V_H + (1-\alpha)V_L). \tag{3.37}$$

By (3.6) and (3.5)

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[(1-(1-\alpha)P_{S_L})(V_L + \alpha(V_H - V_L)]. \tag{3.38}$$

3.6.2 Expected Payoff in SN Plant Population

Similarly to the SS case,

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[E[\omega_S]\alpha(V_H) + E[\omega_N](1-\alpha)(V_L)]. \tag{3.39}$$

By (3.8) and (3.7)

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[P_{N_0}V_L + \alpha(V_H - P_{N_0}V_L)]. \tag{3.40}$$

3.6.3 Expected Payoff in NS Plant Population

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[E[\omega_S](1-\alpha)(V_L) + E[\omega_N]\alpha V_H]. \tag{3.41}$$

By (3.10) and (3.9)

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[(1-P_{S_L})(1-\alpha)V_L + (P_{N_0}+P_{N_H})\alpha V_H] \tag{3.42}$$

$$= R[(1-P_{S_L})V_L + \alpha((P_{N_0}+P_{N_H})V_H - (1-P_{S_L})V_L)]. \tag{3.43}$$

3.6.4 Expected Payoff in NN Plant Population

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[E[\omega_S](0) + E[\omega_N]((\alpha)(V_H) + (1-\alpha)(V_L))]. \tag{3.44}$$

By (3.12) and (3.11)

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[(P_{N_0} + \alpha(P_{N_H})((\alpha)(V_H) + (1-\alpha)(V_L))] \tag{3.45}$$

$$= R[(P_{N_0} + \alpha(P_{N_H})(V_L + \alpha(V_H - V_L))]. \tag{3.46}$$

3.7 Deriving Conditions for SN Dominance

For SN to be a Nash equilibrium, it is sufficient to find the conditions on the parameters in which S dominates N for Pl_H and N dominates S for Pl_L . Namely,

$$\mathscr{E}_{Pl_H}[NN] < \mathscr{E}_{Pl_H}[SN] \tag{3.47}$$

and

$$\mathscr{E}_{Pl_L}[SS] < \mathscr{E}_{Pl_L}[SN] \tag{3.48}$$

respectively.

3.7.1 Conditions for SN be Better than NN for High Yield Plants

By (3.35) and (3.26)

$$\mathscr{E}_{Pl_H}[NN] < \mathscr{E}_{Pl_H}[SN] \tag{3.49}$$

is true when

$$1 - (1 - (P_{N_0} + \alpha P_{N_H}))^{N_B} < 1 - C_H \tag{3.50}$$

$$(1 - (P_{N_0} + \alpha P_{N_H}))^{N_B} > C_H \tag{3.51}$$

$$1 - (P_{N_0} + \alpha P_{N_H}) > C_H^{\frac{1}{N_B}} \tag{3.52}$$

i.e. when

$$1 - C_H^{\frac{1}{N_B}} > P_{N_0} + \alpha P_{N_H}. \tag{3.53}$$

3.7.2 Conditions for SN be Better than SS for Low Yield Plants

By (3.17) and (3.22)

$$\mathscr{E}_{Pl_L}[SS] < \mathscr{E}_{Pl_L}[SN] \tag{3.54}$$

$$(1 - C_L) - ((1-\alpha)P_{S_L})^{N_B} < 1 - (1 - P_{N_0})^{N_B} \tag{3.55}$$

$$-C_L - (1-\alpha)^{N_B} P_{S_L}^{N_B} < -(1 - P_{N_0})^{N_B} \tag{3.56}$$

i.e. when

$$(C_L + (1-\alpha)^{N_B} P_{S_L}^{N_B})^{\frac{1}{N_B}} > (1 - P_{N_0}). \tag{3.57}$$

3.8 SN Dominance

From these derivations we find four condition which are required for SN to be a Nash equilibrium.

$$1 - C_H^{\frac{1}{N_B}} > P_{N_0} + \alpha P_{N_H} \tag{3.58}$$

$$(C_L + (1-\alpha)^{N_B} P_{S_L}^{N_B})^{\frac{1}{N_B}} > 1 - P_{N_0}. \tag{3.59}$$

Now, considering the pollinator's payoff for SN case, given by equation (3.40),

$$\mathscr{E}_{Pol}[P_{S_L}, P_{N_0}, P_{N_H}] = R[P_{N_0}V_L + \alpha(V_H - P_{N_0}V_L)] \tag{3.60}$$

$$= R[(1-\alpha)P_{N_0}V_L + \alpha V_H]. \tag{3.61}$$

It is strictly increasing with P_{N_0}. So it is in the pollinator's benefit to choose P_{N_0} as high as possible. By definition, the pollinator should choose $P_{N_0} = 1$.

However, when $P_{N_0} = 1$ inequality (3.58) is never satisfied. Thus SN cannot be a Nash equilibrium.

CHAPTER IV

BIOLOGICAL CONCLUSION

Pollinators walk a fine line in their attempt to condition their resource providers. The more likely they are to visit non-signaling plants, the less incentive high yield plants have to signal; while the less likely they are to visit non-signaling plants, the more likely low yield plants are to attempt deception in order to be visited.

While our result seems to indicate that an honest system of communication cannot be established between plants and pollinators, we feel this is a reflection of the absence of a crucial feature in our model. One such flaw can be found in the pollinator's payoffs. In the model, a pollinator is allowed to visit R plants through the course of the game. When a pollinator chooses to skip a plant, the model treats this as visiting one of the R flowers and receiving a payoff of 0. As it stands, if a pollinator decides to skip a plant it is essentially leaving resources behind. In reality, pollinators choosing to skip a flower do not expend as much energy as it does visiting. A more realistic model would allow the pollinator to replay the round, a finite number of times; one of the R rounds is concluded when the pollinator visits the plant or surpasses some threshold of skips.

In essence, the pollinator is playing the "One-shot" version of the game R times. In each of the individual rounds, it is always better to visit than skip.

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