Semester Report
8^{th} Semester

Game Theoretic Modeling of Alternative Reproductive Tactics

Submitted by
C L Srinivas
Roll Number: - 2111147
National Institue of Science Education and Research,
Bhubaneswar

Under the guidance of
Dr. Rittik Deb

School of Biological Sciences
NATIONAL INSTITUTE OF SCIENCE EDUCATION AND RESEARCH,
BHUBANESWAR

Semester Report, 8^{th} Semester

Contents

1 Introduction

Reproduction is a fundamental life process, all living things reproduce. It is an understatement to say that reproduction is an important step in the life cycle of an organism. For lower, asexually reproducing organisms, this is a rather straightforward process of budding, fission, regeneration, or vegetative propagation. Higher multicellular organisms, on the other hand, rely on sexual reproduction, which involves the fusion of haploid male and female gametes, thus allowing nature to manifest one of the countless different allelic combinations. Unlike asexual reproduction, sexual reproduction mandates the co-localization and interaction of two separate individuals, who must find each other successfully, within their limited lifespans in their vast and dangerous habitat, generation after generation. Needless to say, this affair is energetically costly, risky, and non-trivial. This unison of male and female individuals of a species to procreate (mating) is mediated by, among other things, mechanisms such as mate signaling and mate choice. Mate signaling is the process by which an individual attracts a member of the opposite sex by means of producing some sort of signal (acoustic, visual, chemical etc.). Mate choice is the act of choosing a "desirable" mate by the opposite sex, based on the quality of the mating signal (Ryan, Akre, and Kirkpatrick 2007; Krebs and Davies 2009). Like most morphological and physiological traits, traits that affect mate signaling and mate choice have inherent variation and are heritable.

These heritable traits, mediators of such a crucial life process, are inevitably subjected to selection. Selection in these contexts will operate in two dimensions; **natural selection** will act along the survivability and fitness axis, and **sexual selection** will act along the reproductive success axis. This is because reproductive fitness can be decomposed into "survivabilty" and "reproductive success", both of which contribute towards the lifetime reproductive success of an individual. And in sexually reproducing organisms, certain traits involved in mate signaling and mate choice are pushed in opposite directions by the two opposing selection forces viz. sexual selection and natural selection. Hence, in such systems we observe trade offs between survivorship and reproductive capacity (**krebs**). As a consequence of sexual selection, there is a great skew in the reproductive success among the individuals of one sex (the sex that experiences the selection, as opposed to the sex that "chooses"). In other words, a small minority of individuals deemed "desirable" by the opposite sex get majority of the reproductive opportunities and the large minority of individuals get little to no reproduction (Figure 1).

As a consequence, natural selection will favor behavioral tactics employed by "undesirable" individuals that are aimed at reducing this inherent skew in reproductive success. Such behavioral tactics are called **Alternative Reproductive Tactics** or **ARTs** for short (Oliveira, Taborsky, and Brockmann 2008). For example, in numerous fish species, males either establish and defend territories in order to gain mating access to the resident females or alternatively choose to employ a "sneaker tactic" whereby they mimic a female and occupy another male's territory and opportunistically mate with resident females. Very sneaky indeed! (Oliveira, Taborsky, and Brockmann 2008) (Figure 2) ARTs can be broadly classified into two categories; genetically determined and condition dependent. Genetically determined ARTs, true to their name are genetically determined at birth, i.e. the individual is predisposed to use that particular ART throughout their life. On the contrary, condition dependent ARTs are those that can be modulated and conditionally employed as an when required by the individuals (Schradin 2019).

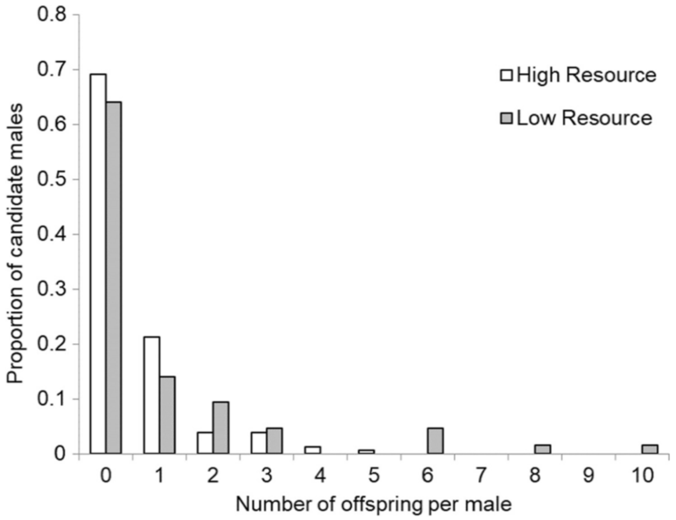


Figure 1: Plot showing the reproductive skew among male *Xerus inauris* from Manjerovic et al. 2022.

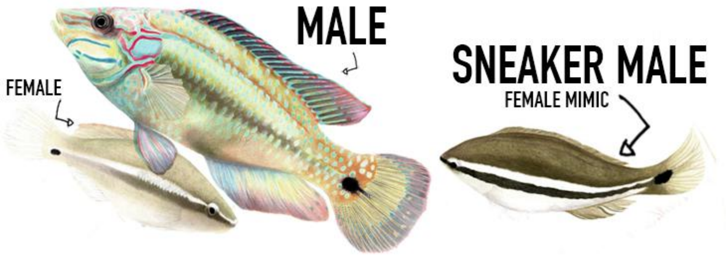
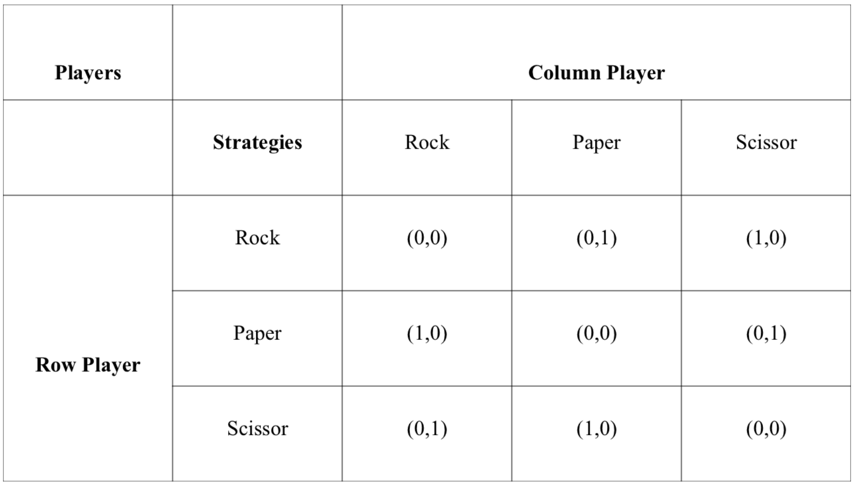


Figure 2: Normal male, sneaker male and female phenotypes in *Symphodus ocellatus*. Illustration by Clara Lacy

The primary motivation behind this study is the desire to understand the evolutionary dynamics of ARTs. This endeavor warrants the use of some rather unconventional techniques, namely **game theory**. This is because conventional evolutionary analysis tools/methods such as parent offspring correlations, heritability and genetic models, whilst well suited for analysis of morphological or physiological traits, are difficult to employ/use for behavioral traits. This is because behavioral traits are a) usually influenced by thousands of genes and environmental factors which means that genetic models are unhelpful, b) change throughout the lifetime of an individual and have a learning component to it which means estimating heritability is difficult and c) have fitness functions that show frequency dependence (both simple and sometimes compound dependence). What we need is a framework that formally defines an interaction between two agents in terms of their behavior during the interaction and the benefits gained/loss incurred thereby as a function of the behaviors used and elicited. Game theory happens to do just that! It defines a game as an interaction between two (or more) players with each player using a well defined sequence of acts called a “strategy”. A payoff value is assigned for each strategy pair and player, this defines the relative benefit/loss of using a particular “strategy” against another in a game.



Players		**Column Player**		
	Strategies	Rock	Paper	Scissor
Row Player	Rock	(0,0)	(0,1)	(1,0)
	Paper	(1,0)	(0,0)	(0,1)
	Scissor	(0,1)	(1,0)	(0,0)

Figure 3: The figure depicts the all too familiar game of rock-paper-scissor as a formal game using the matrix representation of a game. This is also called a 'payoff matrix'.

2 Game theory

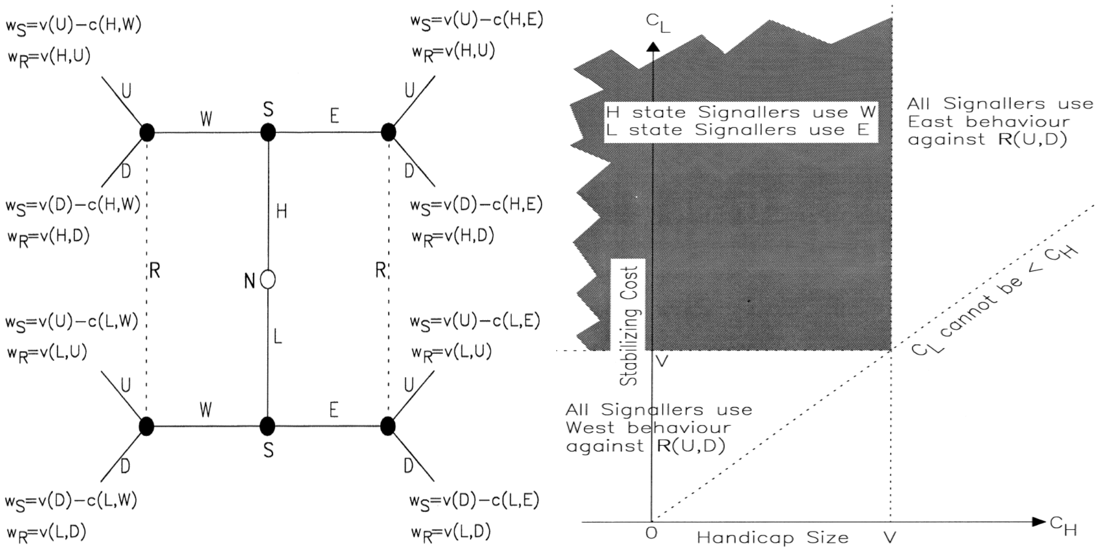
2.1 Game theory and evolution

Game theory is a mathematical discipline that has its roots in the social sciences; initially pioneered as a tool to analyze and optimize economic cum socio-political policies, game theory introduced a mathematical way of looking at strategic interactions between agents, with a well-defined goal of maximizing "payoff" to the player of interest. An example of a simple game is provided in Figure 3.

Behavioral evolutionary biologists quickly realized the scope of game theoretic modeling of behavioral evolution and started to model behavioral phenomena in the animal world as games. The analysis of these games revealed fundamental insights about their evolutionary dynamics. The application of game theory to evolutionary biology spawned into existence the field of evolutionary game theory (Dugatkin and Reeve 2000). Evolutionary game theory, akin to other analytical methods used to understand dynamic processes, tries to find whether equilibrium states exist and if they exists how many and the nature of these states. In terms of evolutionary game theory, equilibrium states are analogous to **Evolutionarily Stable Strategies (ESS)**. This is because ESS is defined as the strategy, which, when employed by all individuals of a population, results in a scenario whereby no other strategy can invade the population. In other words, the population is said to be at equilibrium, when all individuals in the population are using the/an ESS. We can also look at this fact from Fisher's perspective, where, at ESS equilibrium the population is at a peak in the fitness landscape and hence natural selection cannot push it to move further.

2.2 Communication game

A game specifically relevant to my thesis is the **communication game**. We will start by looking at very simple instance of such a game; the **discrete action response game** from Hurd 1995. The game is defined as follows; there is a signaler and a receiver. We define a property called the intrinsic state of the signaler $z \in \{H, L\}$, where H corresponds to high



(a) (b)

Figure 4: a) The game represented in extensive form. (w_s, w_r) denotes the payoffs to the signaler and the receiver respectively, b) A pair of cost parameters (C_H, C_L) specifies a point in the plane of all possible versions of this game for any particular V. The lines $C_H = V$ and $C_L = V$ divide the plane into four different areas around the point V, V. In the shaded area honest signaling is an ESS, where $S(W, E)$ is the best reply to $R(U, D)$ (Hurd 1995)

quality and L corresponds to low quality. The signaler produces a signal $s \in \{W, E\}$ and the receiver reacts with a response $r \in \{U, D\}$, where W elicits the "favorable" response U from the receiver and E elicits the unfavorable response D from the receiver. All the possible states of this game can then be represented using the extensive form of this game as shown in Figure 4a. We assume that signal production entails certain costs and that these costs are a function of both the signal type and the intrinsic state of the signaler, i.e. $c(X, Y)$ denotes the cost of producing a signal Y for a signaler of intrinsic state X. Now, we define marginal costs C_L and C_H as follows;

$$C_L = c(L, W) - c(L, E)$$

$$C_H = c(H, W) - c(H, E)$$

The benefit obtained by a signaler upon eliciting a response r is assumed to be a function of r alone, represented by $\nu(r)$. V is defined as the relative benefit of the response U, where

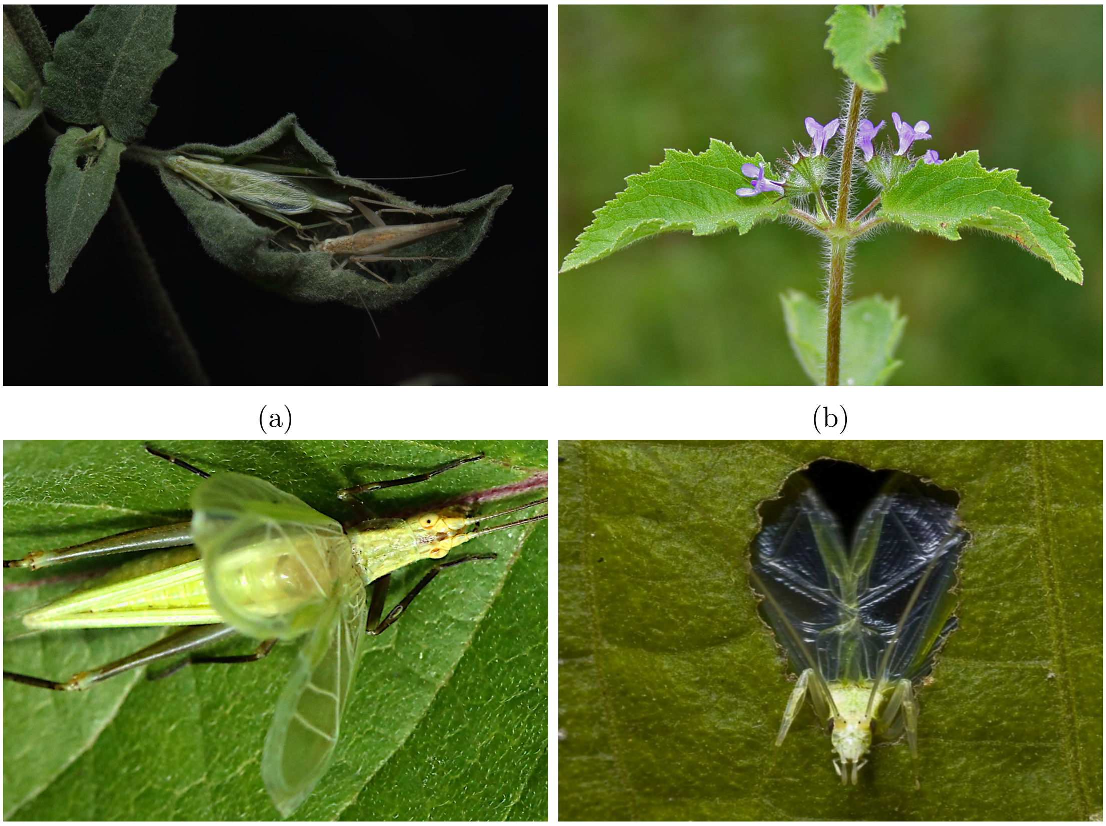
$$V = \nu(U) - \nu(D)$$

All versions of this discrete action response game can then be plotted as a function of C_L and C_H for any fixed value of V (Figure 4b).

It is easy to see that **mate signaling and mate choice behavior between males and females can be modeled as a communication game**, and that is exactly what we aim to do in the model system of our choice; *Oecanthus henryi*.

3 The tree cricket *Oecanthus henryi as a model organism*

Oecanthus henryi (O.henryi) (Figure 5a) is a species of tree cricket abundantly found across most of peninsular India and in our campus. They are found exclusively on their host plant *Hyptis suaveolens*, a weed spread throughout India (Figure 5b). They feed and lay their eggs on this plant. Individuals range from around 9mm to 15mm long and weigh around 18mg to 30mg (from the data I collected during my 2023 summer internship). Adult morphs of this species posses wings; which the males use to produce sound in a process called stridulation (Figure 5c). During this process, males hold their wings erect and perpendicular to their body axis and rub them together. This causes the grooved file of one wing to rub against the smooth plectrum of the other, causing the membranous plectrum to vibrate making a sound (Forrest 1982). Males produce mating calls to attract females. Females perform phonotaxis to locate and mate with suitable males.

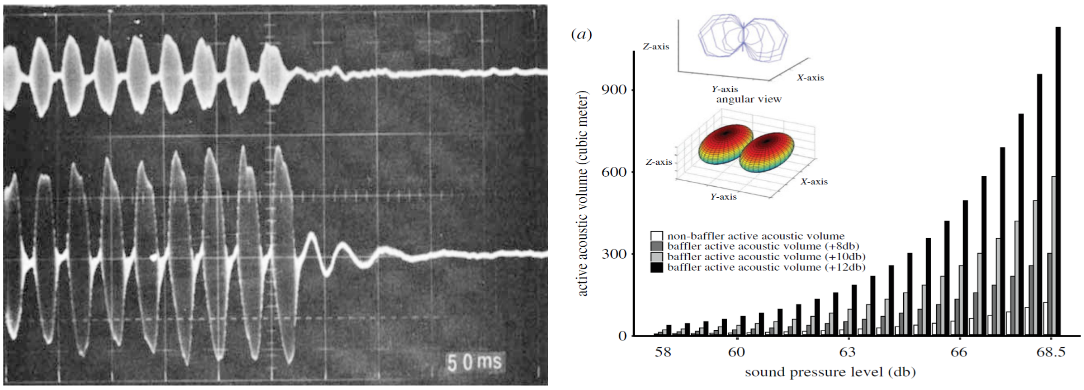

(a) (b)

(c) (d)

Figure 5: a) An *Oecanthus henryi* male (right) and female (left), b) The host plant *Hyptis suaveolens* c) A male *O.henryi* stridulating, d) An *O.henryi* male baffling

3.1 Mate signaling and phonotaxis behavior in *Oecanthus henryi*

The vibrating membrane of the cricket's wings acts as a dipole source of sound, due to a natural phenomenon known as acoustic short-circuiting, the pressure waves at the edges of the wings cancel each other out, leading to a decrement in loudness or Sound Pressure Level (SPL, expressed in dB) (Forrest 1982; Mhatre et al. 2017). In order to overcome this short-circuiting, some *O.henryi* males perform what is known as **baffling** (Figure 5d). This is a behavior wherein a male calls from within a self made hole in a leaf. In this process, the leaf surface acts as an acoustic amplifier, preventing the destructive interference of pressure waves at the wing edges, leading to an increase in call SPL and **acoustic volume** (Figure 6) (Deb, Modak, and Balakrishnan 2020). Acoustic volume is the 3D space around the calling male within which he would be audible to a prospective mate.

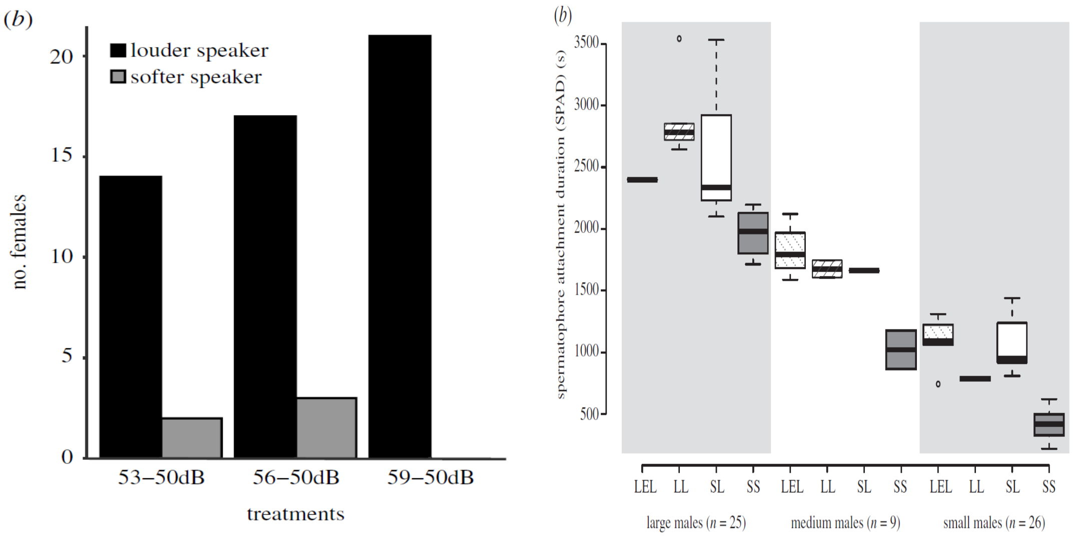


(a) (b)

Figure 6: a) Plot from Prozesky-Schulze et al. 1975 of an oscillogram showing two chirps of *Oecanthus burmeisteri*; upper trace, without baffle and lower trace, using a baffle, b) Plot from Deb, Modak, and Balakrishnan 2020 showing active acoustic volume as a function of call SPL and the increment in active acoustic volume when using a baffle. Data obtained from simulation results.

There is a variation in the loudness of mating calls produced by *O.henryi* males; some males are naturally louder than others. Even though this variation is a continuum, for ease of understanding we will refer to only two classes of males with respect to their natural call loudness - “loud” callers and “soft” callers. Previous studies have indicated that females prefer louder callers (Figure 7). This preference manifests itself in two independent ways; firstly, females choose louder callers to mate with by preferentially locating and moving towards the loudest caller (Figure 7a). Secondly, females have been observed to mate for longer duration with loud males. Technically it is referred to as **Spermatophore Attachment Duration (SPAD)** (Figure 7b) (Deb, Modak, and Balakrishnan 2020). It is evident to see that *O.henryi* use call SPL as a signal to communicate with females who in turn use this signal to choose a desirable mate. There is a communication game going on between *O.henryi* males and females, and hence this interaction can be modeled as such. It is also reasonable to assume that there are significant energy costs associated with producing these mating calls and that these costs scale proportionately with the amplitude, or in this case, the SPL of the signal. Biological signaling theory or Zahavi’s handicap principle (A. Zahavi 1977; Amotz Zahavi 1975) predicts that signal must be costly for honesty to be maintained. Under these contexts, I want to ask and answer the following questions:

1. How can we model this interaction between *O.henryi* males and females as a communication game? What are the strategies and payoffs?



(a) (b)

Figure 7: a) Plot from Deb, Modak, and Balakrishnan 2020 showing female response in a two-choice call playback experiment. The plot shows that greater number females choose the louder speaker (black bars) in each of the three loudness combinations, b) Plot from Deb, Modak, and Balakrishnan 2020 showing the variation of SPAD as a function of both male body size and call SPL. In the experiment, a pre-recorded male call is played back through speakers and the female test subject is allowed to mate with the respective male (whose call was played back) if it manages to successfully locate and move towards the speaker. SS, SL, LL and LEL refers to soft caller's call played back through speaker without manipulation, soft caller's call played back by enhancing its loudness to mimic baffling, loud caller's call played back without manipulation and loud caller's call played back by enhancing its loudness to mimic baffling. As can be seen the playbacks follow an ascending order with respect to SPL when arranged SS<SL<LL<LEL. Corresponding to this we can observe a linear increase in SPAD as we move across SS, SL, LL and LEL in each of the four male body size classes.

2. How does baffling, as an ART, fit into this model and what can we predict about the reproductive tactic of choice for loud and soft males under these settings?

3.2 Honesty and cheating: Mate signaling and female choice in *O.henryi* as a discrete action response game

3.2.1 An honest world without baffling

Here I present a very simplistic model for mate signaling and response in *O.henryi* as a discrete action response game between males and females adapted and modified from Hurd 1995 (Figure 8). We represent a male's physiological energy level using a hypothetical variable called the intrinsic state $z \in \{H, L\}$, where 'H' denotes "high" and 'L' denotes "low". The strategy set for a male is as follows;

$$S_M = \{(60dB, H), (45dB, L), (45dB, H), (60dB, L)\}$$

The strategy (xdB, y) refers to the act of calling (producing a signal s) at a loudness of 'x'dB given the inrinsic energy state 'y'. A female responds to a signal by deciding to mate with the signaler for some duration, this duration or response is denoted by $r \in \{\text{spad}, \text{SPAD}\}$, where spad $<$ SPAD. For any non trivial case, the female must

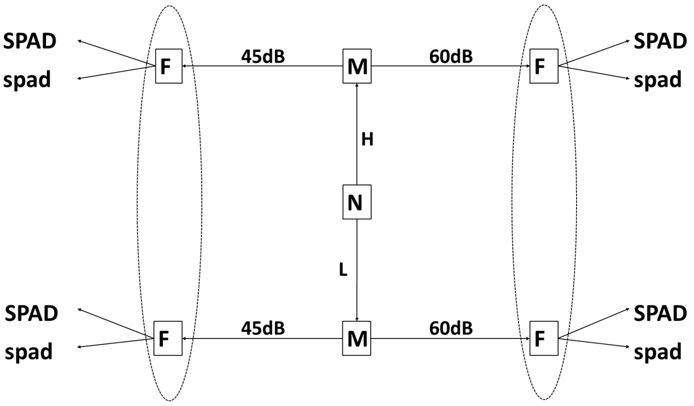


Figure 8: The discrete action-response game between a male signaler and a female receiver in its extensive form. Dotted ellipses enclose the states of the game that form an **Information Set** for the female. All the states of the game that belong to an information set, contain exactly the same information from the receivers point of view and hence the response to each state will be identical to the other. Note that nature (N) first assigns/determines the physiological energy level of a male signaler.

respond variably to different signals, assuming that the females respond favorably to louder signals, we define the female strategy s_F;

$$s_F = \{(45dB, \text{spad}), (60dB, \text{SPAD})\}$$

We assume that it is most beneficial for a female to mate longer with 'high' energy status males and shorter duration with 'low' energy status males. Mathematically, this is;

$$w_F(\text{spad}, L) > w_F(\text{SPAD}, L)$$

$$w_F(\text{SPAD}, H) > w_F(\text{SPAD}, L)$$

where, $w_F(x, y)$ is the fitness benefit to the female when she uses the strategy 'x' against a male of energy status 'y'. The signaler's fitness w_M is a function of both the female response r and the cost of signal production $c(s, z)$.

$$w_M = \nu(r) - c(s, z)$$

The relative benefit of SPAD over spad denoted by V is simply;

$$V = \nu(\text{SPAD}) - \nu(\text{spad}) \tag{1}$$

$$V > 0$$

Assuming that for "low" energy status males, the fitness cost due to energy expenditure during calling at 60dB outweighs the benefit V, we have the following inequality;

$$\nu(\text{spad}) - c(45dB, L) > \nu(\text{SPAD}) - c(60dB, L) \tag{2}$$

Assuming the contrary to be true for "high" energy status males, we have;

$$\nu(\text{SPAD}) - c(65dB, H) > \nu(\text{spad}) - c(45dB, H) \tag{3}$$

We define marginal costs C_H and C_L where C_H denotes the marginal cost of producing a 60dB call for a "high" energy status male and C_L denotes the marginal cost of producing a 60dB call for a "low" energy status male. From (1), (2) and (3), we have;

$$C_H < V < C_L \tag{4}$$

All versions of this game can be plotted as a function of C_H and C_L for a given value of V (Figure 9). It is clear from Figure(9) that the game lies in the domain where the ESS for males is honest signaling of their intrinsic state, i.e. $\{(60dB, H), (45dB, L)\}$ Thus, we can see that honest communication is an ESS in the absence of baffling as an ART.

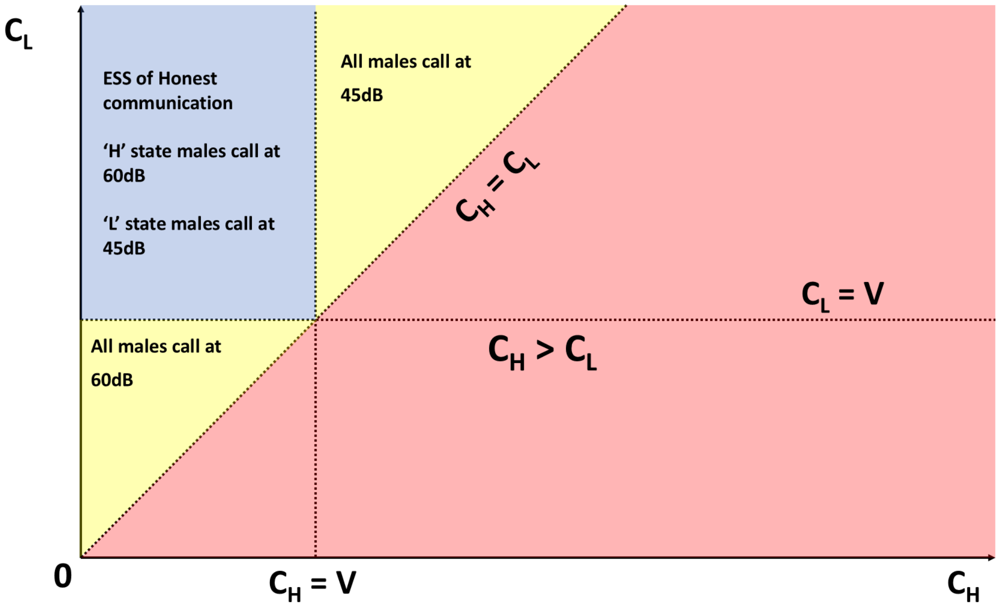


Figure 9: A pair of marginal costs C_H, C_L specifies a point in the plane, in the absence of baffling we can see that the game lies in the blue shaded region where honest signaling is an ESS

3.2.2 The alternative reproductive tactic of baffling as a cheating strategy

Now, let us consider the case where the male strategy set consists of an option to call from a self made baffle hole, in which case the call amplitude is increased. We assume, based on some previous empirical data, an increment of +15dB when baffling. The act of making a baffle however is not without its costs, which will be discussed later in section **??**. The modified male strategy set is S_M;

$$S_M = \{((45dB, \text{call}), H), ((60dB, \text{call}), H), ((60dB, \text{baffle}), H), ((75dB, \text{baffle}), H),$$
$$((45dB, \text{call}), L), ((60dB, \text{call}), L), ((60dB, \text{baffle}), L), ((75dB, \text{baffle}), L)\}$$

The strategy $((xdB, \text{call}), Y)$ and $((xdB, \text{baffle}), Y)$ corresponds to calling at an SPL of 'x'dB and baffling at an SPL of 'x'dB for a given intrinsic state of Y respectively. The new cost function can now be decomposed into a linear sum of two distinct component functions;

$$c((xdB, y), z) = c_0(xdB, z) + c_1(y, z)$$

$$c_1(x, z) = \begin{cases} 0, & \text{if } (x, z) = (\text{call}, L) \\ 0, & \text{if } (x, z) = (\text{call}, H) \\ C'_L, & \text{if } (x, z) = (\text{baffle}, L) \\ C'_H, & \text{if}(x, z) = (\text{baffle}, H) \end{cases}$$

where, c_0 is the fitness cost function associated with the energy expenditure of sound production and c_1 is the fitness cost function associated with the energy expenditure of baffle making. We define,

$$C_H = c_0(60dB, H) - c_0(45dB, H)$$

$$C_L = c_0(60dB, L) - c_0(45dB, L)$$

$$C^*_L = C_L + C'_L$$

$$C^*_H = C_H + C'_H$$

The possible moves for a male and female in this game is schematically represented in figure 10. Additionally, we define,

$$V' = \nu(SPAD^*) - \nu(SPAD)$$

$$V^* = V + V'$$

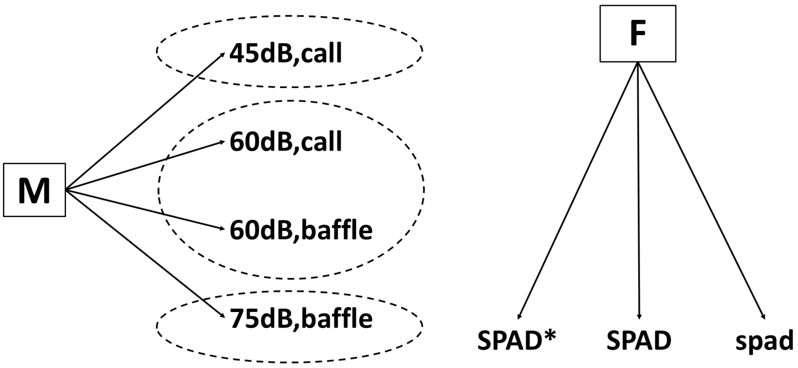


Figure 10: The diagram shows the possible moves for a male and a female cricket in this game. The dotted ellipses contain moves which lead to states that belong to the same information set for the female. spad, SPAD and SPAD* denotes the increasing order of mating duration (female response variable).

Considering the larger size of the strategic space for this game, it would be ideal to analyze the nature of the game under different parameter regimes separately. We can identify these different regimes as characterized by the following relationships between C_H, C_L, C'_H and C'_L:

1. Case I

$$\begin{aligned} C_H &< C'_H \\ C_L &> C'_L \end{aligned} \tag{I}$$

2. CASE II

$$\begin{aligned} C_H &< C'_H \\ C_L &< C'_L \end{aligned} \tag{II}$$

3. CASE III

$$\begin{aligned} C_H &> C'_H \\ C_L &> C'_L \end{aligned} \tag{III}$$

4. CASE IV

$$\begin{aligned} C_H &> C'_H \\ C_L &< C'_L \end{aligned} \tag{IV}$$

3.2.2.1 Case I

Under this regime (I), baffle manufacture is relatively beneficial for L state callers where as it is not so for H state callers. This parameter regime might be close to natural conditions as empirical evidence suggests higher baffling propensity for softer males (L state males) as compared to naturally loud callers (H state males). Under this parameter regime, we can ask the question, what is the ESS for a male? And we can compute the same analytically, by using simple algebra keeping in mind the inequalities that we need to respect. Here are the basic inequalities that we will use throughout all cases,

$$C_L > V > C_H \tag{1}$$

$$V > V' \tag{2}$$

From 1 and 2, WLOG, we have,

$$C_L > V > V' > C_H \tag{3}$$

From I and 3, WLOG, we have,

$$C_L > C'_L > V > V' > C_H \tag{4}$$

$$C_L > V > C'_L > V' > C_H \tag{5}$$

Using I, 4 and 5, WLOG, we have the following four cases,

$$C_L > C'_L > V > V' > C'_H > C_H \tag{Ia}$$
$$C_L > C'_L > V > C'_H > V' > C_H \tag{Ib}$$
$$C_L > V > C'_L > V' > C'_H > C_H \tag{Ic}$$
$$C_L > V > C'_L > C'_H > V' > C_H \tag{Id}$$

CASE IA

For L state signalers, the fitness associated with the different moves are,

$$\begin{aligned} w_m@(45dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\ w_m@(60dB, \text{call}) &= \nu(SPAD) - c_o(60dB, L) \\ w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, L) - c_1(\text{baffle}, L) \\ w_m@(75dB, \text{baffle}) &= \nu(SPAD^*) - c_0(60dB, L) - c_1(\text{baffle}, L) \end{aligned}$$

And comparing the move $(45dB, \text{call})$ with all possible moves,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(\mathit{spad}) - c_0(45dB, L) \\ &\quad - \nu(SPAD) + c_0(60dB, L) \\ &= C_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(\mathit{spad}) - c_0(45dB, L) \\ &\quad - \nu(SPAD) + c_0(45dB, L) \\ &\quad + c_1(\text{baffle}, L) \\ &= C'_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(\mathit{spad}) - c_0(45dB, L) \\ &\quad - \nu(SPAD^*) + c_0(60dB, L) \\ &\quad + c_1(\text{baffle}, L) \\ &= C_L + C'_L - V \\ &= C^*_L - V \\ &> 0 \end{aligned}$$

Thus, $(45dB, \text{call})$ **is the best response for L state signalers.**

For H state signalers, the fitness associated with the different moves are,

$$\begin{aligned} w_m@(45dB, \text{call}) &= \nu(\mathit{spad}) - c_0(45dB, H) \\ w_m@(60dB, \text{call}) &= \nu(SPAD) - c_o(60dB, H) \\ w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, H) - c_1(\text{baffle}, H) \\ w_m@(75dB, \text{baffle}) &= \nu(SPAD^*) - c_0(60dB, H) - c_1(\text{baffle}, H) \end{aligned}$$

We can perform pairwise comparisons of the fitness of different moves for the signaler and compute the best response.

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(\mathit{spad}) - c_0(45dB, H) \\ &\quad - \nu(SPAD) + c_0(60dB, H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &\quad - \nu(SPAD) + c_0(45dB, H) \\ &\quad + c_1(\text{baffle}, H) \\ &= C'_H - C_H \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD^*) + c_0(60dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - V' \\ &< 0 \end{aligned}$$

Thus, under sufficiently high value of V', $(75dB, \text{baffle})$ **is the best response for** H **state signalers. Hence the ESS for a male is** $\{((75dB, \text{baffle}), H), ((45dB, \text{call}), L)\}$.

Case Ib

For L state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(60dB, L) \\ &= C_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(45dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C'_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD^*) + c_0(60dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C_L + C'_L - V \\ &= C^*_L - V \\ &> 0 \end{aligned}$$

Thus, $(45dB, \text{call})$ **is the best response for** L **state signalers.**
For H state signalers however, performing pairwise comparisons of fitness expressions for the different moves,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\ &- \nu(SPAD) + c_0(60dB, H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD) + c_0(45dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - C_H \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB,\text{call}) - w_m@(75dB,\text{baffle}) &= \nu(SPAD) - c_0(60dB,H) \\ &- \nu(SPAD^*) + c_0(60dB,H) \\ &+ c_1(\text{baffle},H) \\ &= C'_H - V' \\ &> 0 \end{aligned}$$

Thus, under relatively low value of V', $(60dB,\text{call})$ **is the best response for H state signalers. Hence the ESS for a male is**
$\{((60dB,\text{baffle}),H),((45dB,\text{call}),L)\}$.

Case Ic

For L state signalers, comparing the move $(60dB,\text{baffle})$ with all possible moves,

$$\begin{aligned} w_m@(60dB,\text{baffle}) - w_m@(45dB,\text{call}) &= \nu(SPAD) - c_0(45dB,L) \\ &- c_1(\text{baffle},L) \\ &- \nu(spad) + c_0(45dB,L) \\ &= V - C'_L \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB,\text{baffle}) - w_m@(60dB,\text{call}) &= \nu(SPAD) - c_0(45dB,L) \\ &- c_1(\text{baffle},L) \\ &- \nu(SPAD) + c_0(60dB,L) \\ &= C_L - C'_L \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB,\text{baffle}) - w_m@(75dB,\text{baffle}) &= \nu(SPAD) - c_0(45dB,L) \\ &- c_1(\text{baffle},L) \\ &- \nu(SPAD^*) + c_0(60dB,L) \\ &+ c_1(\text{baffle},L) \\ &= C_L - V' \\ &> 0 \end{aligned}$$

Thus, $(60dB,\text{baffle})$ **is the best response for L state signalers**.
For H state signalers,

$$\begin{aligned} w_m@(45dB,\text{call}) - w_m@(60dB,\text{call}) &= \nu(spad) - c_0(45dB,H) \\ &- \nu(SPAD) + c_0(60dB,H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB,\text{call}) - w_m@(60dB,\text{baffle}) &= \nu(SPAD) - c_0(60dB,H) \\ &- \nu(SPAD) + c_0(45dB,H) \\ &+ c_1(\text{baffle},H) \\ &= C'_H - C_H \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD^*) + c_0(60dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - V' \\ &< 0 \end{aligned}$$

Thus, under sufficiently high value of V', $(75dB, \text{baffle})$ **is the best response for** H **state signalers. Hence the ESS for a male is** $\{((75dB, \textbf{baffle}), H), ((60dB, \textbf{baffle}), L)\}$**.**

Case Id

For L state signalers,

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(45dB, \text{call}) &= \nu(SPAD) - c_0(45dB, L) \\ &- c_1(\text{baffle}, L) \\ &- \nu(spad) + c_0(45dB, L) \\ &= V - C'_L \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(60dB, \text{call}) &= \nu(SPAD) - c_0(45dB, L) \\ &- c_1(\text{baffle}, L) \\ &- \nu(SPAD) + c_0(60dB, L) \\ &= C_L - C'_L \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, L) \\ &- c_1(\text{baffle}, L) \\ &- \nu(SPAD^*) + c_0(60dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C_L - V' \\ &> 0 \end{aligned}$$

Thus, $(60dB, \text{baffle})$ **is the best response for** L **state signalers**.
For H state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\ &- \nu(SPAD) + c_0(60dB, H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD) + c_0(45dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - C_H \\ &> 0 \end{aligned}$$

$$
\begin{aligned}
w_m@(60dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\
&\quad - \nu(SPAD^*) + c_0(60dB, H) \\
&\quad + c_1(\text{baffle}, H) \\
&= C'_H - V' \\
&> 0
\end{aligned}
$$

Thus, under relatively low value of V', $(60dB, \text{call})$ **is the best response for H state signalers.**
Hence the ESS for a male is $\{((60dB, \textbf{baffle}), H), ((60dB, \textbf{baffle}), L)\}$.
All of these possibilities can be represented using a phase plot as shown in figure 11.

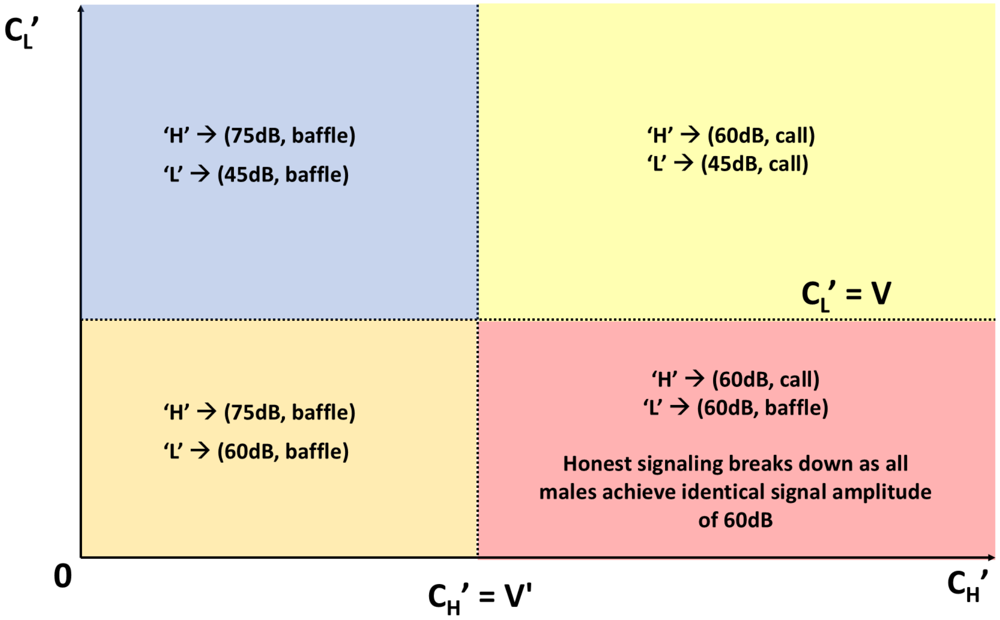


Figure 11: Phase plot depicting all the possible ESS for a male as a function of the parameters C'_L, V', V and C'_H.

3.2.2.2 Case II

Under this regime (II), baffle manufacture is not relatively beneficial for both L and H state callers. This parameter regime might correspond to conditions of low leaf availability, high predation pressure etc. that can drive up baffle manufacturing costs (refer 3.3). Using a similar scheme of analysis, from 1,2 and II, WLOG, we have,

$$C'_L > C_L > V > V' > C_H \tag{3}$$

From 3 and II, WLOG, we have the following two cases,

$$C'_L > C_L > V > V' > C_H > C'_H \tag{IIa}$$
$$C'_L > C_L > V > C_H > V' > C'_H \tag{IIb}$$

CASE IIA

For L state signalers, comparing the move $(45dB, \text{call})$ with all possible moves,

$$\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{call}) &= \nu(spad) - c_0(45dB,L)\\
&- \nu(SPAD) + c_0(60dB,L)\\
&= C_L - V\\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{baffle}) &= \nu(spad) - c_0(45dB,L)\\
&- \nu(SPAD) + c_0(45dB,L)\\
&+ c_1(\text{baffle},L)\\
&= C'_L - V\\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(75dB,\text{baffle}) &= \nu(spad) - c_0(45dB,L)\\
&- \nu(SPAD^*) + c_0(60dB,L)\\
&+ c_1(\text{baffle},L)\\
&= C_L + C'_L - V\\
&= C^*_L - V\\
&> 0
\end{aligned}$$

Thus, $(45dB,\text{call})$ **is the best response for** L **state signalers.**
For H state signalers,

$$\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{call}) &= \nu(spad) - c_0(45dB,H)\\
&- \nu(SPAD) + c_0(60dB,H)\\
&= C_H - V\\
&< 0
\end{aligned}$$

$$\begin{aligned}
w_m@(60dB,\text{call}) - w_m@(60dB,\text{baffle}) &= \nu(SPAD) - c_0(60dB,H)\\
&- \nu(SPAD) + c_0(45dB,H)\\
&+ c_1(\text{baffle},H)\\
&= C'_H - C_H\\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(60dB,\text{call}) - w_m@(75dB,\text{baffle}) &= \nu(SPAD) - c_0(60dB,H)\\
&- \nu(SPAD^*) + c_0(60dB,H)\\
&+ c_1(\text{baffle},H)\\
&= C'_H - V'\\
&< 0
\end{aligned}$$

Thus $(75dB,\text{baffle})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(45dB,\textbf{call}),L),((75db,\textbf{baffle}),H)\}$.

CASE IIB

For L state signalers, comparing the move $(45dB,\text{call})$ with all possible moves,

$$\begin{aligned}
w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\
&- \nu(SPAD) + c_0(60dB, L) \\
&= C_L - V \\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\
&- \nu(SPAD) + c_0(45dB, L) \\
&+ c_1(\text{baffle}, L) \\
&= C'_L - V \\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(45dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\
&- \nu(SPAD^*) + c_0(60dB, L) \\
&+ c_1(\text{baffle}, L) \\
&= C_L + C'_L - V \\
&= C^*_L - V \\
&> 0
\end{aligned}$$

Thus, $(45dB, \text{call})$ **is the best response for** L **state signalers.**
For H state signalers,

$$\begin{aligned}
w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\
&- \nu(SPAD) + c_0(60dB, H) \\
&= C_H - V \\
&< 0
\end{aligned}$$

$$\begin{aligned}
w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\
&- \nu(SPAD) + c_0(45dB, H) \\
&+ c_1(\text{baffle}, H) \\
&= C'_H - C_H \\
&> 0
\end{aligned}$$

$$\begin{aligned}
w_m@(60dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\
&- \nu(SPAD^*) + c_0(60dB, H) \\
&+ c_1(\text{baffle}, H) \\
&= C'_H - V' \\
&> 0
\end{aligned}$$

Thus $(60dB, \text{call})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(45dB, \textbf{call}), L), ((60db, \textbf{call}), H)\}$.
All of these possibilities can be represented on a phase plot as shown in figure 12

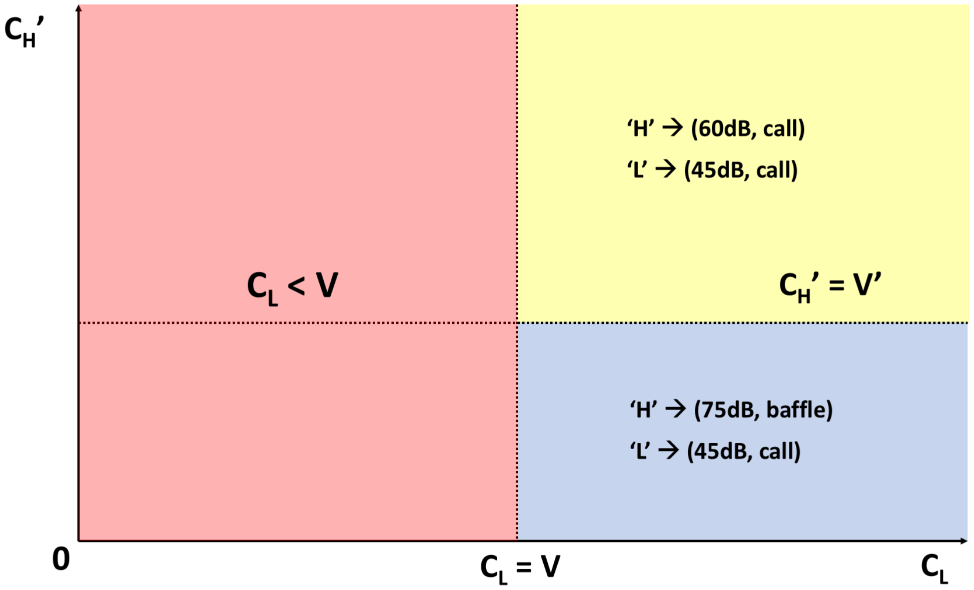


Figure 12: Phase plot depicting all the possible ESS for a male as a function of the parameters C_L, V', V and C'_H.

3.2.2.3 Case III

Under this parameter regime (III), baffling is relatively beneficial for males of all status. This might correspond to a scenario of abundance of large leaves, minimal predation pressure etc. that can minimize baffling manufacturing costs (refer 3.3). Extending the method of analysis used in previous sections, from 1, 2 and III, we have WLOG,

$$C_L > V > V' > C_H > C'_H \tag{3}$$
$$C_L > V > C_H > V' > C'_H \tag{4}$$

From 3, 4 and III we have the following four cases,

$$C_L > C'_L > V > V' > C_H > C'_H \tag{IIIa}$$
$$C_L > V > C'_L > V' > C_H > C'_H \tag{IIIb}$$
$$C_L > C'_L > V > C_H > V' > C'_H \tag{IIIc}$$
$$C_L > V > C'_L > C_H > V' > C'_H \tag{IIId}$$

CASE IIIA

For L state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(60dB, L) \\ &= C_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(45dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C'_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(75dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD^*) + c_0(60dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C_L + C'_L - V \\ &= C^*_L - V \\ &> 0 \end{aligned}$$

Thus, $(45dB, \text{call})$ **is the best response for** L **state signalers.** For H state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\ &- \nu(SPAD) + c_0(60dB, H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD) + c_0(45dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - C_H \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, H) \\ &- c_1(\text{baffle}, H) \\ &- \nu(SPAD^*) + c_0(60dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C_H - V' \\ &< 0 \end{aligned}$$

Thus $(75dB, \text{baffle})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(45dB, \textbf{call}), L), ((75dB, \textbf{baffle}), H)\}$.

CASE IIIB

For L state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(60dB, L) \\ &= C_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(45dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C'_L - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, L) \\ &- c_1(\text{baffle}, L) \\ &- \nu(SPAD^*) + c_0(60dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C_L - V' \\ &> 0 \end{aligned}$$

Thus, $(60dB, \text{baffle})$ **is the best response for L state signalers.**
For H state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\ &- \nu(SPAD) + c_0(60dB, H) \\ &= C_H - V \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\ &- \nu(SPAD) + c_0(45dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C'_H - C_H \\ &< 0 \end{aligned}$$

$$\begin{aligned} w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, H) \\ &- c_1(\text{baffle}, H) \\ &- \nu(SPAD^*) + c_0(60dB, H) \\ &+ c_1(\text{baffle}, H) \\ &= C_H - V' \\ &< 0 \end{aligned}$$

Thus $(75dB, \text{baffle})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(60dB, \textbf{baffle}), L), ((75dB, \textbf{baffle}), H)\}$.

Case IIIc

For L state signalers,

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(60dB, L) \\ &= C_L - V \\ &> 0 \end{aligned}$$

$$\begin{aligned} w_m@(45dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(spad) - c_0(45dB, L) \\ &- \nu(SPAD) + c_0(45dB, L) \\ &+ c_1(\text{baffle}, L) \\ &= C'_L - V \\ &> 0 \end{aligned}$$

$$
\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(75dB,\text{baffle}) &= \nu(spad) - c_0(45dB,L)\\
&\quad - \nu(SPAD^*) + c_0(60dB,L)\\
&\quad + c_1(\text{baffle},L)\\
&= C_L + C'_L - V\\
&= C^*_L - V\\
&> 0
\end{aligned}
$$

Thus, $(45dB,\text{call})$ **is the best response for** L **state signalers.**
For H state signalers,

$$
\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{call}) &= \nu(spad) - c_0(45dB,H)\\
&\quad - \nu(SPAD) + c_0(60dB,H)\\
&= C_H - V\\
&< 0
\end{aligned}
$$

$$
\begin{aligned}
w_m@(60dB,\text{call}) - w_m@(60dB,\text{baffle}) &= \nu(SPAD) - c_0(60dB,H)\\
&\quad - \nu(SPAD) + c_0(45dB,H)\\
&\quad + c_1(\text{baffle},H)\\
&= C'_H - C_H\\
&< 0
\end{aligned}
$$

$$
\begin{aligned}
w_m@(60dB,\text{baffle}) - w_m@(75dB,\text{baffle}) &= \nu(SPAD) - c_0(45dB,H)\\
&\quad - c_1(\text{baffle},H)\\
&\quad - \nu(SPAD^*) + c_0(60dB,H)\\
&\quad + c_1(\text{baffle},H)\\
&= C_H - V'\\
&> 0
\end{aligned}
$$

Thus $(60dB,\text{baffle})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(45dB,\textbf{call}),L),(60dB,\textbf{baffle}),H)\}$.

CASE IIId

For L state signalers,

$$
\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{call}) &= \nu(spad) - c_0(45dB,L)\\
&\quad - \nu(SPAD) + c_0(60dB,L)\\
&= C_L - V\\
&> 0
\end{aligned}
$$

$$
\begin{aligned}
w_m@(45dB,\text{call}) - w_m@(60dB,\text{baffle}) &= \nu(spad) - c_0(45dB,L)\\
&\quad - \nu(SPAD) + c_0(45dB,L)\\
&\quad + c_1(\text{baffle},L)\\
&= C'_L - V\\
&< 0
\end{aligned}
$$

$$\begin{aligned}
w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, L) \\
&- c_1(\text{baffle}, L) \\
&- \nu(SPAD^*) + c_0(60dB, L) \\
&+ c_1(\text{baffle}, L) \\
&= C_L - V' \\
&> 0
\end{aligned}$$

Thus, $(60dB, \text{baffle})$ **is the best response for L state signalers.** For H state signalers,

$$\begin{aligned}
w_m@(45dB, \text{call}) - w_m@(60dB, \text{call}) &= \nu(spad) - c_0(45dB, H) \\
&- \nu(SPAD) + c_0(60dB, H) \\
&= C_H - V \\
&< 0
\end{aligned}$$

$$\begin{aligned}
w_m@(60dB, \text{call}) - w_m@(60dB, \text{baffle}) &= \nu(SPAD) - c_0(60dB, H) \\
&- \nu(SPAD) + c_0(45dB, H) \\
&+ c_1(\text{baffle}, H) \\
&= C'_H - C_H \\
&< 0 \\
w_m@(60dB, \text{baffle}) - w_m@(75dB, \text{baffle}) &= \nu(SPAD) - c_0(45dB, H) \\
&- c_1(\text{baffle}, H) \\
&- \nu(SPAD^*) + c_0(60dB, H) \\
&+ c_1(\text{baffle}, H) \\
&= C_H - V' \\
&> 0
\end{aligned}$$

Thus $(60dB, \text{baffle})$ **is the best response for H state signalers.** Hence the **ESS for a male is** $\{(60dB, \textbf{baffle}), L), ((60dB, \textbf{baffle}), H)\}$. All of these possibilities can be represented on a phase plot as shown in figure 13

3.2.2.4 Case IV

Under this parameter regime (IV), baffling is relatively beneficial only for males of high energy status. This scenario, whilst mathematically feasible, does not match anything we know or hypothesize about the behavior of *O.henryi*. For purposes of simplicity, this case was not analyzed, however one can obtain phase plots similar to those obtained above for this case as well.

3.3 Costs and benefits of baffling

The literature on *O.henryi* ecology, behavior and the condition dependent ART of baffling shed some light on the costs and benefits of this behavioral tactic. Given below is a concise overview of the important insights. A diagrammatic representation of the same is given in Figure 14.

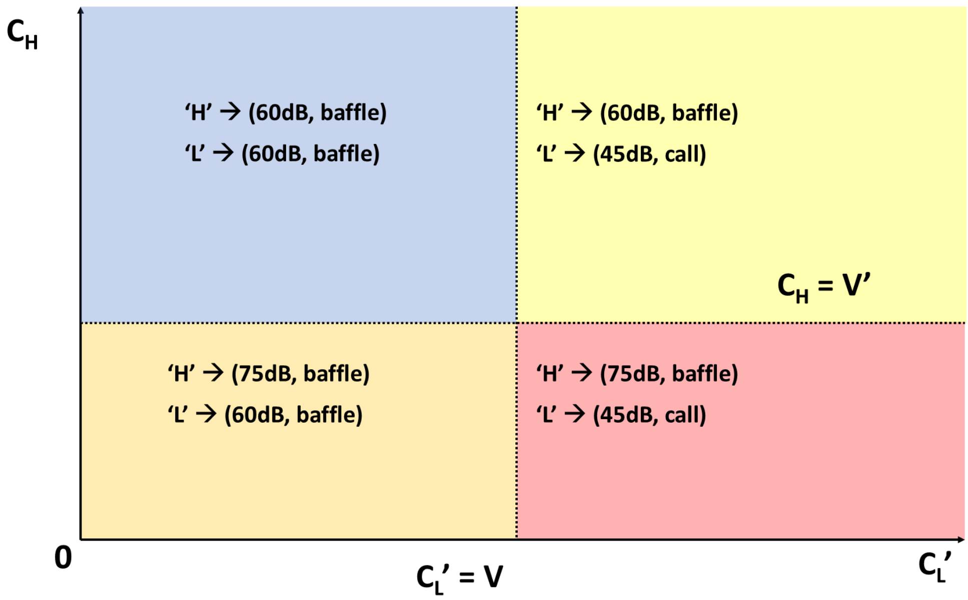


Figure 13: Phase plot depicting all the possible ESS for a male as a function of the parameters C_L, V', V and C'_H.

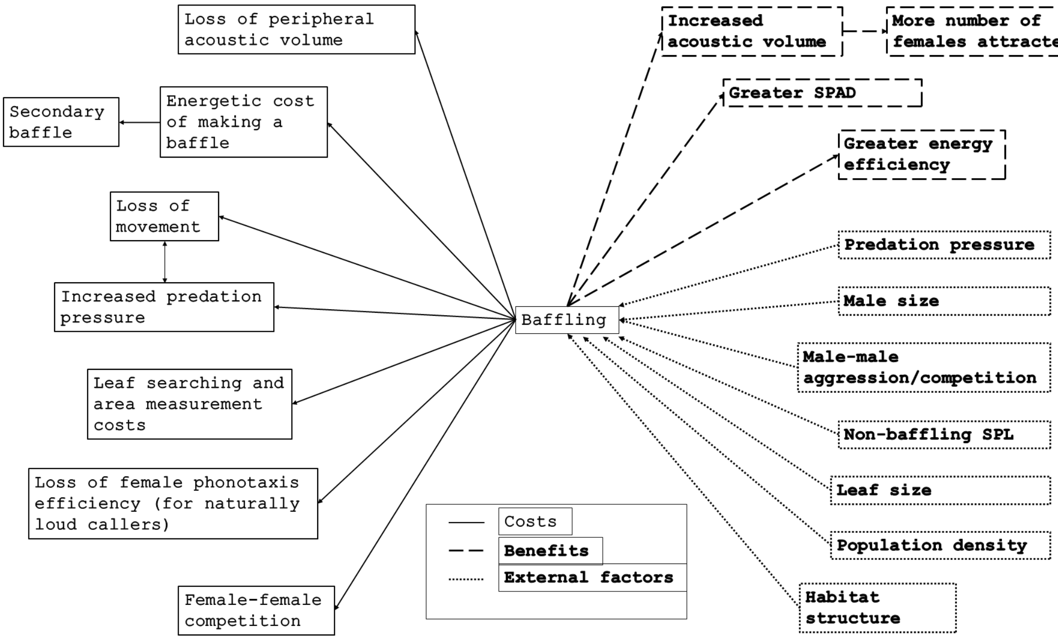


Figure 14: A schematic representation of the factors that affect the costs and benefits of baffling.

3.3.1 Costs

1. **Loss of peripheral acoustic volume: -** Investigation into the optimizations involved in baffle making using finite element modeling by Mhatre et al. 2017 reveal that while the sound field is intensified in the anterior-posterior axis of the cricket, the peripheral or lateral acoustic volume does not experience significant gain in SPL. Thus, baffling entails a loss of peripheral acoustic volume by polarizing and amplifying the acoustic volume along the anterior-posterior axis of the calling male.

2. **Energetic cost of making a baffle: -** The very act of baffle making a baffle on a given leaf might not be an energy inexpensive process, especially since *O.henryi* males are known to optimize baffle hole size and shape to maximize acoustic amplification. This optimization might entail multiple iterations of calling through the incomplete baffle ⟶ baffle modifications ⟶ calling again. Additionally, *O.henryi* males are also known to make multiple baffle holes on the same leaf. In the case that the initial baffle hole is not optimally positioned, *O.henryi* males will sometimes make another baffle hole on the same leaf in order to increase the efficiency of the baffle (Mhatre et al. 2017). This bi-layered optimization involved in baffle making (one of size and one of position) might make it an all the more costlier behavior.

3. **Loss of movement: -** Making a baffle is tantamount to fixing ones position for the entire duration of calling (Sadiq et al. 2024), since making a baffle is a costly affair, its unlikely for the male to abandon it within the night. This can have multiple drawbacks:

    (a) **Loss of chance mating: -** Individual based modeling by Sadiq et al. 2024 showed that movement confers an increase in mating success to calling and silent males in structured habitats. In fact, mobile calling males out-compete stationary bafflers in structured habitats. Thus, loss of random, opportunistic matings is also a fitness cost that can be attributed to baffling as an alternative strategy.

    (b) **Increased predation risk: -** Even though there are no empirical evidences to show that bafflers are at higher predation risk due to increased active acoustic volume, we hypothesis that loss of movement can contribute to this end. Essentially, bafflers are sitting ducks for prospective predators who, we assume, can hone in on a stationary target much more easily than onto a mobile one.

4. **Increased predation risk: -** Bafflers may experience higher predation risk through effects independent from loss of mobility. Crickets use their antennae to surveil their surroundings; including scanning for predators. A baffle hole is very restrictive structure that does not permit 360^o antennal, visual or auditory surveillance of the environment. This might increase the predation risk for bafflers as compared to non-baffling males.

5. **Leaf search and area measurement costs** Previous studies have shown that there is a correlation between leaf area and baffling propensity (Deb, Modak, and Balakrishnan 2020); indicating that *O.henryi* males do not choose leaves to make baffle holes randomly. We hypothesis that *O.henryi* males measure leaf surface area and selectively choose to baffle on relatively larger leaves. Several methods of leaf area measurement have been hypothesized and tested by Kumar n.d.. Among the hypothesis, one in particular, involving Singing At Leaf Edge (SALE) can be noted as being very energetically costly. This behavior consists of calling from the edge of the leaf whose area is to be measured, listening to ones own call and compute the area of the leaf based on auditory feedback. This hypothesis was tested and ruled out due to physical considerations of the call wavelength being larger than resonator size (in this case the cricket (12mm)) and the fact that some cricket species have been shown to be deaf their own calls. However, this auditory de-sensitization mechanism

has not been shown to exist in *Oecanthus henryi* and empirical observations in our lab indicate otherwise.

6. **Loss of female phonotaxis efficiency: -** For naturally loud males, baffling can have detrimental effects as their call amplitude might surpass the normal hearing threshold of conspecific females. This detrimental effect of excessive loudness has been indicated in phonotaxis experiments performed in the laboratory by Deb, Modak, and Balakrishnan 2020 where females took longer time to locate and move towards speakers playing back male calls at very high SPL.

7. **Female-female competition: -** Simulation based studies have shown that naturally loud males who call from baffle holes tend to attract more females than they can mate with within one night (Deb, Modak, and Balakrishnan 2020). Thus, we hypothesize that female-female competition might actually reduce a loud baffler's nightly reproductive success as compared to calling without baffle.

3.3.2 Benefits

1. **Increased acoustic volume: -** Prior studies have clearly established the increment in call SPL and active acoustic volume when calling through a baffle using both observation and simulation data (Deb, Modak, and Balakrishnan 2020).

2. **Increased number of females attracted: -** As a direct consequence of increased active acoustic volume, bafflers attract greater number of females per night as compared to callers. This was explicitly shown through simulation data by Deb, Modak, and Balakrishnan 2020.

3. **Greater Spermatophore Attachment Duration: -** It is known that females provide higher SPAD to louder males, hence through baffling, males increase their SPAD per mating, leading to greater reproductive success (Deb, Modak, and Balakrishnan 2020).

4. **Greater energy efficiency: -** Considering that a baffle works like an acoustic amplifier, baffling increases Sound Radiating Efficiency (SRE) (Mhatre et al. 2017), thus reducing the marginal cost for signal production per unit increase in SPL.

3.3.3 Factors that affect baffling propensity

1. **Predation pressure: -** Since we already saw that baffling might increase the risk of predation, the fitness cost associated with this behavior would be a function of the existing predation pressure.

2. **Male body size: -** Deb, Modak, and Balakrishnan 2020 have shown that there is a strong correlation between male body size and baffling propensity, with larger males being less likely to baffle. This could be due to physiological reasons; large bodied males might have larger fat deposits and energy stores that allow them to bear the high energetic cost of calling without significant fitness costs. The same cannot be said for small bodied males however, hence the propensity to baffle.

3. **Male-male aggression/competition: -** Currently, there is no evidence to the existence of hostile/aggressive interactions between *O.henryi* males. However, we hypothesis that there could be such aggressive interactions that could drive up the risk/fitness cost of baffling, by attracting aggressive conspecific males.
4. **Leaf size: -** Previous studies have shown that leaf size affects baffling propensity where larger leaves are more likely to be used to make baffles (Deb, Modak, and Balakrishnan 2020).
5. **Population density: -** Individual based modeling and simulations by Sadiq et al. 2024 show that population density plays an important role in mediating the negative frequency dependence of the fitness benefit of baffling on the proportion of bafflers in the population.
6. **Habitat structure: -** Habitat structuring refers to structural elements in the habitat that dictate the spatial distribution of individuals in the habitat. In this case, a 'structured habitat' refers to one with bushes of the host plant *O.henryi* as opposed to a homogeneous habitat which would be devoid of such structural elements. Individual based modeling has shown that habitat structuring negatively affects the fitness benefit of the baffling tactic (Sadiq et al. 2024).

3.4 A Further Realistic Extension of this model

Hitherto, we have considered the payoffs for a signaling male with respect to its interaction with a single receptive female. Furthermore, we have not considered the effect of another male intrinsic feature that is known to affect female preference; namely, body size. We can augment our model to ensure that the the male intrinsic state z is now a tuple such that $z = (x, y)$ where y denotes a males body size and x denotes its energy status. An accurate depiction of the male's payoff therefore, should be a product of the number of receptive females and the payoff of a single mating event with a receptive female (which should ideally be a function of both the perceived loudness of the signal and the male body size). One way to model this is by imagining nature as an intermediary between the signaler and receiver. Nature as a player, makes a move in order to determine the number of females a particular signaling male will attract as a response to the specific signal made. This game is represented in the normal form in figure 15.

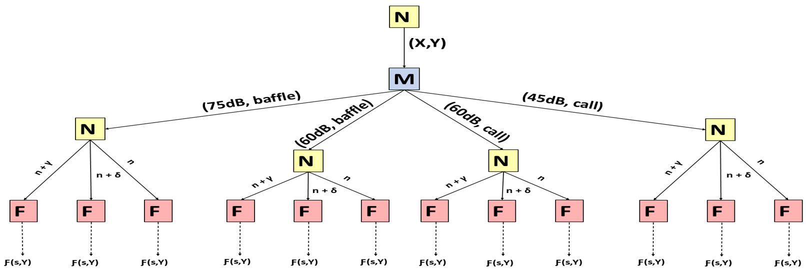


Figure 15: The sequential game with nature as an intermediary in its normal form. n denotes the number of females attracted by a signal of 45dB and δ and γ represent the increments to this quantity as the signal loudness increases to 60dB and 75dB. $F(s, y)$ denotes the mating benefit from a single mating to a male of size y using a signal s.

4 Future Plans

4.1 Understanding and quantifying the costs/benefits associated with baffling and how these parameters affect the nature of the communication game and the ESS strategies

Essentially, a game is specified by the marginal costs/benefits involved. These marginal parameters are dictated by the cost/benefits of baffling behavior and the external factors that affect them. Hence by quantifying these costs and benefits in terms of fitness values, we can predict the state of the game and hence the ESS to be expected.

4.2 Generate testable predictions from the models and validate them through laboratory experiments

By plugging in conservative estimates for the cost and benefit terms in these models and from simulations that can be run based on this framework, we can generate testable hypothesis about the population, individual behavior etc. I would like to generate such predictions and put them to the test using controlled laboratory experiments.

4.3 Generalize the discrete action response game into its continuous version

Currently, the discrete action-response model does not do justice to the range of variation present in signaling strategies and responses possible in real life. Ideally, the strategy set and response should be real, continuous, finite intervals. Hence, in future I would like to generalize this discrete game into its continuous version and investigate how it affects the evolutionary stable states.

5 Bibliography

References

Deb, Rittik, Sambita Modak, and Rohini Balakrishnan (Dec. 2020). “Baffling: A Condition-Dependent Alternative Mate Attraction Strategy Using Self-Made Tools in Tree Crickets”. In: *Proc. R. Soc. B.* 287.1941, p. 20202229. ISSN: 0962-8452, 1471-2954. DOI: `10.1098/rspb.2020.2229`. (Visited on 01/11/2025).

Dugatkin, Lee Alan and Hudson Kern Reeve (2000). *Game Theory and Animal Behavior.* Oxford: Oxford University Press. ISBN: 978-0-19-513790-3 978-0-19-535020-3.

Forrest, T. G. (Mar. 1982). “Acoustic Communication and Baffling Behaviors of Crickets”. In: *The Florida Entomologist* 65.1, p. 33. ISSN: 00154040. DOI: `10.2307/3494144`. JSTOR: `3494144`. (Visited on 01/11/2025).

Hurd, Peter L. (May 1995). “Communication in Discrete Action-Response Games”. In: *Journal of Theoretical Biology* 174.2, pp. 217–222. ISSN: 0022-5193. DOI: `10.1006/jtbi.1995.0093`. (Visited on 01/11/2025).

Krebs, John R. and Nicholas B. Davies (July 2009). *Behavioural Ecology: An Evolutionary Approach.* John Wiley & Sons. ISBN: 978-1-4443-1362-8.

Kumar, Harsha K (n.d.). “Baffling Behavior in the Tree Cricket Oecanthus Henryi: How Is Leaf Area Measured?” In: ().

Manjerovic, Mary Beth et al. (Aug. 2022). “Intraspecific Variation in Male Mating Strategies in an African Ground Squirrel (*Xerus Inauris*)”. In: *Ecol. Evol.* 12.8. ISSN: 2045-7758, 2045-7758. DOI: `10.1002/ece3.9208`. (Visited on 01/14/2025).

Mhatre, Natasha et al. (Dec. 2017). “Tree Crickets Optimize the Acoustics of Baffles to Exaggerate Their Mate-Attraction Signal”. In: *eLife* 6, e32763. ISSN: 2050-084X. DOI: `10.7554/eLife.32763`. (Visited on 01/11/2025).

Oliveira, Rui F., Michael Taborsky, and H. Jane Brockmann (Mar. 2008). *Alternative Reproductive Tactics: An Integrative Approach.* Cambridge University Press. ISBN: 978-1-139-46952-4.

Prozesky-Schulze, L. et al. (May 1975). “Use of a Self-Made Sound Baffle by a Tree Cricket”. In: *Nature* 255.5504, pp. 142–143. ISSN: 0028-0836, 1476-4687. DOI: `10.1038/255142a0`. (Visited on 01/11/2025).

Ryan, Michael J., Karin L. Akre, and Mark Kirkpatrick (May 2007). “Mate Choice”. In: *Current Biology* 17.9, R313–R316. ISSN: 0960-9822. DOI: `10.1016/j.cub.2007.02.002`. (Visited on 02/10/2025).

Sadiq, Mohammed Aamir et al. (June 2024). “Spatial Structure Could Explain the Maintenance of Alternative Reproductive Tactics in Tree Cricket Males”. In: *Biol. Open* 13.6, bio060307. ISSN: 2046-6390. DOI: `10.1242/bio.060307`. (Visited on 01/11/2025).

Schradin, Carsten (2019). “Alternative Reproductive Tactics”. In: *Encyclopedia of Animal Cognition and Behavior.* Springer. (Visited on 01/12/2025).

Zahavi, A. (Aug. 1977). “The Cost of Honesty (Further Remarks on the Handicap Principle)”. In: *J Theor Biol* 67.3, pp. 603–605. ISSN: 0022-5193. DOI: `10.1016/0022-5193(77)90061-3`.

Zahavi, Amotz (Sept. 1975). “Mate Selection—A Selection for a Handicap”. In: *Journal of Theoretical Biology* 53.1, pp. 205–214. ISSN: 0022-5193. DOI: `10.1016/0022-5193(75)90111-3`. (Visited on 01/22/2025).