Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

Micah Allen Brady

Effects of environmental variation on the evolution of pure, conditional and learned social foraging strategies

Master's thesis in Nordic Master of Biodiversity and Systematics
Supervisor: Dr. Jonathan Wright
Co-supervisor: Dr. Thomas Haaland
May 2024

Bob Vuxinic / Project Feeder Watch, Song Sparrows in The Snow

NTNU
Norwegian University of
Science and Technology

Micah Allen Brady

Effects of environmental variation on the evolution of pure, conditional and learned social foraging strategies

Master’s thesis in Nordic Master of Biodiversity and Systematics
Supervisor: Dr. Jonathan Wright
Co-supervisor: Dr. Thomas Haaland
May 2024

Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

NTNU
Norwegian University of
Science and Technology

Contents

List of Figures

List of Tables

1 Abstract

The behavior of animals is influenced by genetic and environmental factors as well as the interactions between the two. It is also influenced by the behavior of others. The Producer-Scrounger model is a classic model that looks at two behaviors in an inverse frequency relationship to predict population level frequencies of tactic usage. Previous studies have conflated learning and non-learning plastic strategies, leading to confusion and a lack of comparison for all possible strategy types. Here, we utilized an agent based model to follow individuals in populations through time, observing genetic changes, strategy choices and levels of producers and scroungers. This model uses a deterministic correlation function to cause variability in the environment in a predictable fashion through the modification of the producers bonus, as well as utilizing an underlying liability reaction norm framework to treat the act of producing or scrounging as a threshold trait. We ran scenarios that allowed and prevented plasticity from evolving. These scenarios varied in how the environment changed over time and how fast. We confirm that the type of environmental fluctuation and its speed has an impact on the types of strategies evolved in a population. In addition, we test learning strategists in an environment with conditional plastic, non-plastic mixed, and pure strategies and confirm that learning strategies can become fixed in a population and are the most successful and numerous in an environment that allows for plasticity to evolve.

Acknowledgment

I would like to acknowledge those who have gotten me to a place I never thought I would be. I sincerely thank them for their support and mentorship.

- Dr.Jonathan Wright, for showing me a completely new way to think about and study science.
- Dr.Thomas Haaland, for always being there when I needed help and whose contributions to this thesis cannot be overstated.
- Dr.Mikael Thollesson and Dr.Petra Korall, for rekindling my love to go out into nature to see what I can find.
- My family, especially my parents Michael and Kathleen Brady, for giving me this great opportunity to cross oceans to further my education.
- My wife Libby, who believed in and encouraged me every day.

2 Introduction

In the course of an individual animal's life it must make many decisions. These decisions range from protection of resources (Grant 1993), if it should fight an opponent, to if it should migrate. Each time a decision needs to be made, it must be made in its own unique context. However, it is not possible for an individual to account for all of the possible variation found in life, and so how behavioral strategies cope with this uncertainty is an important problem. For example, the individual might behave in a way that ensures decent success in a wide range of conditions, or it alter its behavior to better fit the specific context that it finds itself in (Clements and Stephens 1995).

An assumption often made in the field of behavioral ecology is that individuals, through natural selection, evolve optimal strategies for making decisions that maximize fitness (Parker and J. Smith 1990), as the individual that behaves more optimally than its competitors may survive and reproduce more successfully, passing its strategies to the next generation through its genes (Davies et al. 2012, McNamara and Leimar 2020). One way an individual may optimize chances of surviving and reproducing is how it obtains food through its foraging behavior, and an example of this optimization of foraging behavior is the marginal value theorem. In the marginal value theorem, individuals gain private information of the environment through their experiences of the travel time between patches of food and the diminishing returns an individual receives from revisiting a food patch multiple times. Utilizing this information, there exists an optimal amount of visits-made-to/time-spent-at a food patch before the individual should move to a new one (Charnov 1976). An individual using such information to adjust their behavior may gain higher food intake than individuals using a constant strategy.

These decisions are not only made in isolation, as in reality no individual operates in a vacuum and is surrounded by members of both its own and other species from which the individual can obtain public information, in addition to the private information it gathers itself. For social groups, individuals can assess the optimal decisions in various situations by obtaining public information from other group members through a variety of cues, behavioral patterns and signals that can inform the individual of threats, resource availability and locations, hazardous foods and more (Templeton and Luc-Alain Giraldeau 1995, Kacsoh et al. 2018). The information gained from others influences an individual's decisions and their outcomes, having just as much of an impact on the fitness of the individual as environmental factors (Katsnelson, Motro, M. W. Feldman, et al. 2008). In some cases, the common phrase "knowledge is power" could be changed to "knowledge is fitness" as higher quality information can improve individual survival and other fitness enhancing activities.

Individuals don't make one decision in life and will need to make many in a multitude of circumstances and contexts over time, requiring different strategies to navigate each situation in an optimal way. The optimal strategy in the one context may not be as successful in the next. Adopting a strategy that works decently in most cases or optimal in a different environmental context could cause an individual to potentially miss out on resources it could have exploited. One technique to aid an animal in the diverse situations it will encounter in its life is learning. When an animal uses learning, it draws upon the memories of the successes and errors in past experiences to inform the decision it must make in its current context (Harley 1981), granting it the flexibility to both adapt to and succeed in a wider range of contexts. The more experience an individual has and the more it has observed others, the more likely they will be able to make the best possible decision. Katsnelson et al (2011) described learning as a dynamic process involving stochastic sampling errors that influence subsequent sampling steps, and eventually produce a wide distribution of possible outcomes (Katsnelson, Motro, M. Feldman, et al. 2011). By encountering and more importantly remembering errors in its own judgement or remembering observed errors in others, an individual using learned strategies can select against tactics that previously produced a negative or lackluster outcome in environmental contexts it has already experienced.

As mentioned before no individual acts in a vacuum. There are other individuals that interact with both the environment and the initial individual. Game Theory is used to study these interactions where the rewards of an individuals actions or decisions are dependent on the actions and decisions of other individuals in the game (J. M. Smith 1982). As stated in Table 1 games consist of 1 or more rounds where distinct actions or behaviors are known as "tactics" are played by individuals. In round 1 of a game, an individual might choose to play tactic "A" out of a set of tactics ["A","B"]. An example of a tactic in a social context is where one member of a conspecific group moves to a high position and watches for threats while other members forage/graze (Bednekoff 1997).

Strategies are precise descriptions of what tactic an individual will use in a given situation or state (flee when you encounter something that eats you). The importance of strategies to the evolution of populations and species is that they are the basic unit through which selection acts (McNamara and Leimar 2020) because the strategies an individual employs will determine its reproductive success. The effectiveness of a strategy will be demonstrated by the proportion of the population that utilizes it as more successful strategies will spread through the population. Strategies can vary in the number of tactics they consist of and how tactics are chosen. Pure strategies employ one tactic for each possible situation. Mixed strategies have many tactics played in different conditions or at different probabilities. Conditional strategies integrate information to determine what tactic should be selected in each case and can be extremely diverse.

2.1 ESS

In theory there are an infinite number of strategies that can be employed, but we often only observe one in a population, the evolutionary stable strategy (J. M. Smith 1982). The Evolutionary Stable Strategy (ESS) as described by Maynard Smith (1982) is the strategy most stable under natural selection because if a majority of a population adopts it, no "mutant" strategy can invade and give a higher reproductive fitness. The ESS can be fixed or plastic ('conditional'), and can be a universal ('pure') strategy that every individual uses or can be a ('mixed') combination of different pure strategies played by individuals used in the same population. (Maynard Smith 1974). Fixed strategies simply use one tactic in all situations. A mixed strategy involves one or more tactics that are each chosen a proportion of the time. A conditional plastic strategy samples the environment at that moment in time

Term	**Definition**
Private information	Information obtained by an individual through its own experiences. Here, comparison of payoffs of playing alternative tactics (eq. 5)
Public information	Information available to all individuals that can be observed from the surroundings. Here, tracking the numbers of producers and scroungers in the population (eq. 6)
Game Theory	Mathematical modeling approach involving two or more individuals with competing or aligning interests, where the tactics played by one individual are influenced by acts played by the other. Games consist of 1 or more rounds, moves or time steps where each individual plays 1 tactic a round from a set of available acts
Tactic	In Game theory, a discrete act played by the individual during a time step in the game. Manifests in animal populations as a phenotype or behavior displayed
Decision rule	A description of the relationship between an internal or external stimulus and the choices an individual makes
Strategy	In Game theory, a set of decision rules for a sequence of tactics played by the individual for the duration of the game. Each chosen tactic is selected based on decision rules and can depend on an organism's internal state (e.g. body condition, informational state), the (social) environment, etc.
"Simple" or "Pure" Strategies	A strategy only using either one tactic or the other, so individuals do not alternate between them.
"Complex" or "Mixed" Strategies	A strategy playing a specified combination of different tactics at different probabilities
"Fixed" or Non-Plastic Strategy	A strategy that plays the same tactic or combination of tactics regardless of the environment
"Conditional" or Plastic Strategy	A strategy played by an individual that that displays different tactics in different environmental conditions and incorporates information about the payoffs of alternative tactics
ESS	A strategy (tactic or mixture of tactics) that, once adopted by a population, cannot be invaded by any other mutant strategy. In a game there may be more than one ESS. ESSs are properties of populations and not individuals
Pure ESS	An ESS in which each individual plays only one tactic
Mixed ESS	An ESS in which each individual randomly plays one or both of the alternative tactics, such as fight with probability p and sneak with probability 1—p, or through a genetically polymorphic evolutionary stable state in which different individuals play different strategies within the population
Conditional ESS	An ESS that operates through a mechanism (physiological, neurological, or developmental) that detects appropriate cues and plastically alters the strategy
Phenotypic plasticity	The ability of single genotypes to produce different phenotypes in different environments based on informative cues
Learning	The ability to use the memory of past payoffs of strategies played by the individual or others to alter the current strategy
Behavioral Reaction Norm	Graphical depiction of the relationship between an expressed behavior or phenotype and different environmental conditions
Liability	An underlying genetic or environmental trait that determines the displayed phenotype depending if it is above or below a certain threshold
Liability Reaction Norm	Graphical depiction of the relationship between liability of a trait across various environments
Animal personality	Consistent differences between individuals in their behaviour across time and contexts. This implies that interindividual correlations exist in behaviour across time or contexts (also referred to as 'behavioural syndromes')
Continuous trait	A trait that is continuously distributed on observed phenotypic scale.
Threshold trait	A trait that shows two (or more) discrete phenotypic states, where phenotypic expression directly depends on the value of an underlying "liability" relative to a threshold. Individuals above the threshold display one tactic while individuals below the threshold(s) display an alternate morph

Table 1: Glossary of terms adapted from J. M. Smith 1982, Dingemanse et al. 2010, Reid and Acker 2022, Roff et al. 1997, Dugatkin and Reeve 1998, Modelling Animal Decisions Group: et al. 2014

to make a decision on which particular tactic to use. Plastic learning is distinguished from other plastic strategies in that it uses memory of past experiences to influence its decision and is useful in a stochastic environment and/or where high quality information for sampling is unavailable.

2.2 Frequency dependent populations in Producer-scrounger social games

A population can consist of multiple individuals adopting different strategies. When this occurs, the strategies played by individuals interact with each other and can affect their overall success in a way not seen with the strategies in isolation. An example of a game theory model that incorporates interacting strategies is the producer-scrounger model. Developed in the early 1980s (Barnard and Sibly 1981). Using captive house sparrows, the producer-scrounger model involves a population with two mutually exclusive tactics: 'Producers', individuals that search for and discover new food patches, and 'Scroungers', individuals that forage at food patches that have already been discovered by producers. The payoffs of these tactics are frequency dependent, where the success of each is linked to the proportion of each tactic being played in the population. When most of the population is composed of producers, it is more advantageous to be a scrounger, and vice-versa. The ESS, i.e the ratio of tactic use at which producer and scrounger payoffs are equal is also affected by other factors, such as group size (Vickery et al. 1991) and distribution of food patches (Beauchamp 2008). Empirical studies show that other factors not related directly to resource availability, like genetic relatedness, dominance, predation risk, allocation of food among scroungers, and time of day also can have an impact on the population's ESS (Tóth et al. 2009, Katsnelson, Motro, M. W. Feldman, et al. 2008, T. Caraco et al. 1989, Coolen and Luc-Alain Giraldeau 2003, Lendvai et al. 2004).

A key parameter controlling the ESS proportion of scroungers is the amount of food from a patch a producer can eat before scroungers join and food is shared, known as the producer bonus, or finder's share Tóth et al. 2009. Namely, an increase in the producer bonus leaves less food for possible scroungers and lowers the average proportion of individuals playing the scrounger tactic. This empirical result agrees with the prediction of theoretical models with static, rate-maximizing environments (Vickery et al. 1991, Thomas Caraco and Giraldea 1991). However, the dynamic model by Barta and Luc-Alain Giraldeau 2000 suggests that in a changing environment, higher levels of scroungers can be found at these same share values than are predicted by the static model.

Many older models of the producer scrounger game are deterministic and static (Barnard and Sibly 1981, Vickery et al. 1991). These models make the assumption that the act of foraging for food is used to replace energy lost throughout the day, that there is only one rate of obtaining energy, and that individuals focus on achieving the maximum rate of fitness and obtaining energy over time, and making predictions on behavior based on this one rate (Thomas Caraco and Giraldea 1991). The environments these models take place in do not take into account temporal variation in energy acquisition nor the threat of death from starvation and the urgency both place on foraging individuals (Thomas Caraco and Giraldea 1991).

Models like the those found in Beauchamp 2008, utilize an agent-based approach involving stochastic simulation models, where each individual has its entire life cycle and social interactions with others modeled. Following an individual through timesteps allows for an environment that changes over time, producing a variance in the ability of individual to gain food and avoid starvation. Experimental studies like Houston and McNamara 1987 suggest that in order to fulfill energy requirements, individuals will forgo a strategy that gains more food on average in the long term for a strategies that fulfills their immediate requirement,and that optimum behaviors rely not only on the mean energy intake, but the energetic state of the individual. Empirical studies like Young et al. 1990 and Thomas Caraco, Martindale, et al. 1980 support this theory. An agent-based approach gives the researcher access to reliable information and enables them to explore the effects more stochastic food availability have on an ESS. This allows the model to handle situations that are more similar to those we find in nature than the deterministic analytical models. More recently, some modelling studies have begun using the producer-scrounger game to study the evolution of learning in game-theoretical contexts, including Dubois, Morand-Ferron, et al. 2010 and Katsnelson, Motro, M. Feldman, et al. 2011. The two studies have differing techniques and therefore slightly different results.

Dubois, Morand-Ferron, et al. 2010 utilizes a mathematical model approach, and deliberately looks at the outcome of learning while ignoring the underlying mechanisms of learning. The model begins with a population of individuals using fixed strategies in equilibrium, followed by the introduction of a mutant learning individual and observation of its fate. In this study, learning happens instantaneously with no time lag or storage of information, and a learner always chooses the most profitable of three possibilities: producer, scrounger, or a given combination that alternates as a set rate. Dubois, Morand-Ferron, et al. 2010 refer to these individuals as using a mixed strategy as they are more akin to the usage of conditional plastic strategies than that of learning, as there is no memory involved and the environment is assumed to be perfectly sampled to choose the most productive strategy in that situation. When the mean populations of producers and scroungers are observed, the "learning" individuals are included in the count with fixed individuals.

The Dubois et al. (2010) study suggests that “learning individuals will play a pure producer tactic, regardless of initial conditions” because the first learning individual to play against individuals with fixed strategies will optimize its own allocation of food and favor a mixture of tactics that tends to include a higher ratio of producer tactic to scrounger. This causes a feedback loop leading fixed individuals to adopt scrounger exclusive tactics in the next generation, leading to learning individuals to use the producer tactic even more. At a certain point, these "learning" strategies are simply not viable and are unlikley to become fixed in the population, especially if the learners assess the the payoffs of alternate strategies. “Learners can do better than fixed producers or fixed scroungers, but never better than both” (Dubois, Morand-Ferron, et al. 2010).

Katsnelson et al. (2011) use an agent-based approach to observe how the phenomenon of learning, expressed as a linear operator (LO) rule, can evolve to fixation in a population, depending on environmental conditions and degree of phenotypic asymmetry (differences in their ability to succeed with a chosen strategy stemming from various possible origins). This study tests two learning rules under 4 payoff types to observe their effect on the learned strategy choice. These learning rule test cases were used in two populations. The first being a population of pure strategists at equilibrium, with a learning gene added later. The second population tested was composed of non-learners all using a mixed strategy and “coin flipping” to choose their tactics with equal probabilities. In this study, contrary to Dubois, Morand-Ferron, et al. 2010, the learning strategy was able to become fixed in the population of pure strategists and was “consistently successful in invading a population of mixed strategy players” when the player phenotypes were asymmetric(Katsnelson, Motro, M. Feldman, et al. 2011).

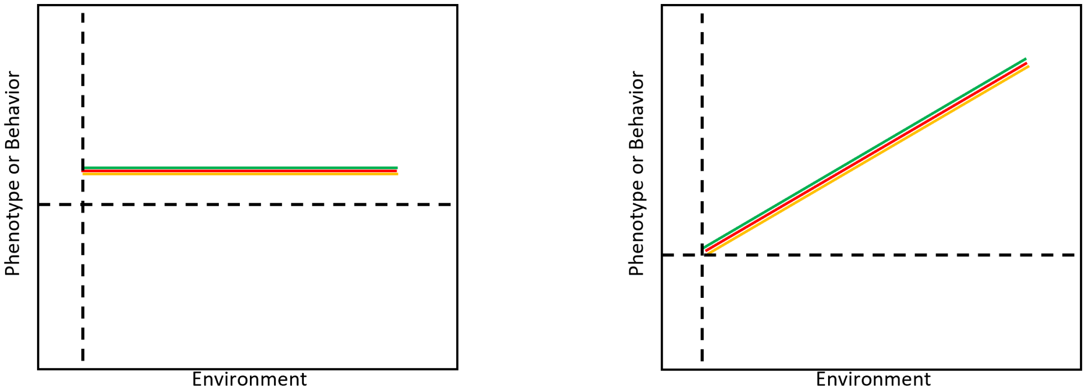
2.3 Types of information in the Producer/Scrounger game

An individual in a game is privy to two types of information, public and private, as defined in table 1. In the producer-scrounger game the choice of tactics (whether to produce or scrounge) can utilize any information about the environment. Private information about the payoffs of different tactics is obtained each time a tactic is chosen. Public information is obtained when an individual assesses the social environment(Valone 1989), but it is unknown if each information type is more beneficial under certain conditions.

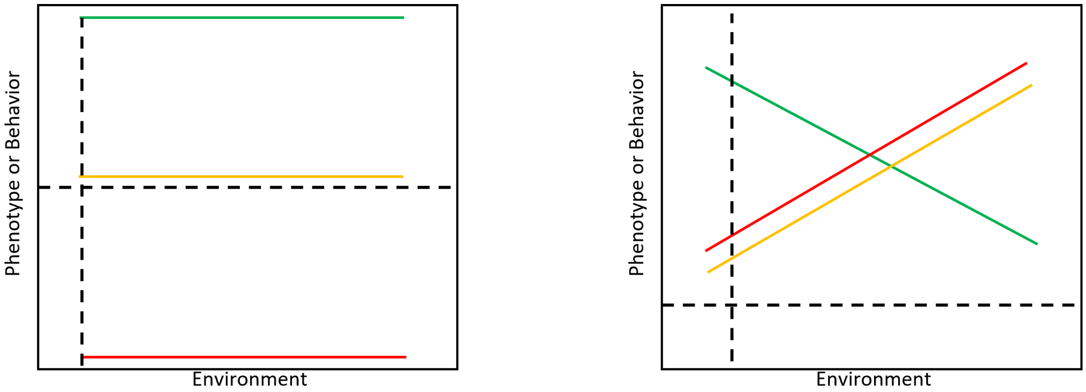
3 Behavioral Reaction norms and Liabilities

3.1 Behavioral Reaction Norms

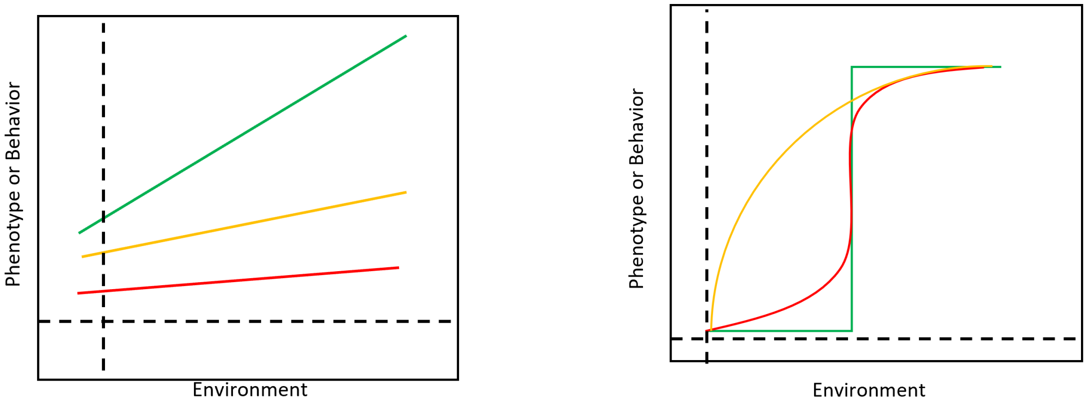
To visualize the range of phenotypes an individual expresses in response to a given stimulus or environment it is typical to utilize a Behavioral Reaction Norm (BRN) approach to show an individual’s response to different environmental conditions. The elevation, slope, and shape of the line allows the identification of different animal personalities and behavior types. Personality in animals is defined as a consistent difference between individuals in their behavior across time and contexts, implying that there are interindividual correlations that exist (Dingemanse et al. 2010). A simple example is shown in figure 1c. All three individuals express the same level of plasticity (none), but express different mean levels of behavior. Because of that, these individuals show consistent differences across different environmental contexts and can be labeled as having different personalities. Figure 1 showcases different behavioral types and personalities for a group of three hypothetical individuals in a changing environment.



(a) Non-plastic BRNs (b) Plastic BRNs

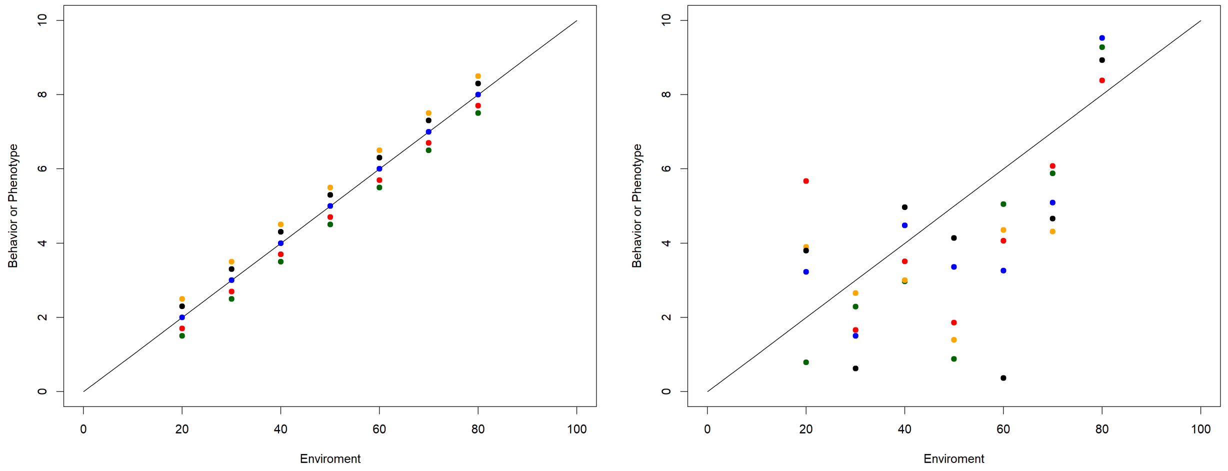


(c) Non-plastic BRNs with differing personalities (d) Plastic BRNs with differing personalities



(e) Plastic BRNs with different levels of plasticity (f) BRNs with non-linear shapes

Figure 1: Examples of Behavioral reaction norm shapes



(a) High Phenotypic Precision

(b) Low Phenotypic Precision

Figure 2: Examples of Phenotypic precision

While these BRNs aid in understanding and even predicting animal behavior, this assumes perfect phenotypic precision or low phenotypic noise. Phenotypic precision describes how closely the expressed phenotypes of an individual follows the phenotype predicted by its genotype (David. F. Westneat et al. 2019, Hansen et al. 2006). Inversely, phenotypic noise or phenotypic variance describes the random deviation individual phenotypes might show from the predicted phenotype of a reaction norm. The amount of noise or variance an individual displays can be affected by selection and is not universal amongst individuals (Orzack and Sober 1994), nor does it consist of the same components (David F. Westneat et al. 2015). The effect of this random noise is that it is the inverse of repeatability, a commonly used measure in behavioral studies detailing consistency amongst individuals over multiple observations in the same environment (Bell et al. 2009). If one were to record the phenotypic reactions of a group of individuals with high phenotypic precision or low noise, one would see results similar to figure 2a where 7 observations of 5 individuals are both clustered near the reaction norm and show a repeated, predictable pattern amongst eachother. In contrast, observing individuals with low phenotypic precision or high noise would give results more similar to figure 2b where the 5 individuals are spread across the behavioral space amongst 7 observations and show different patterns to each other and the BRN.

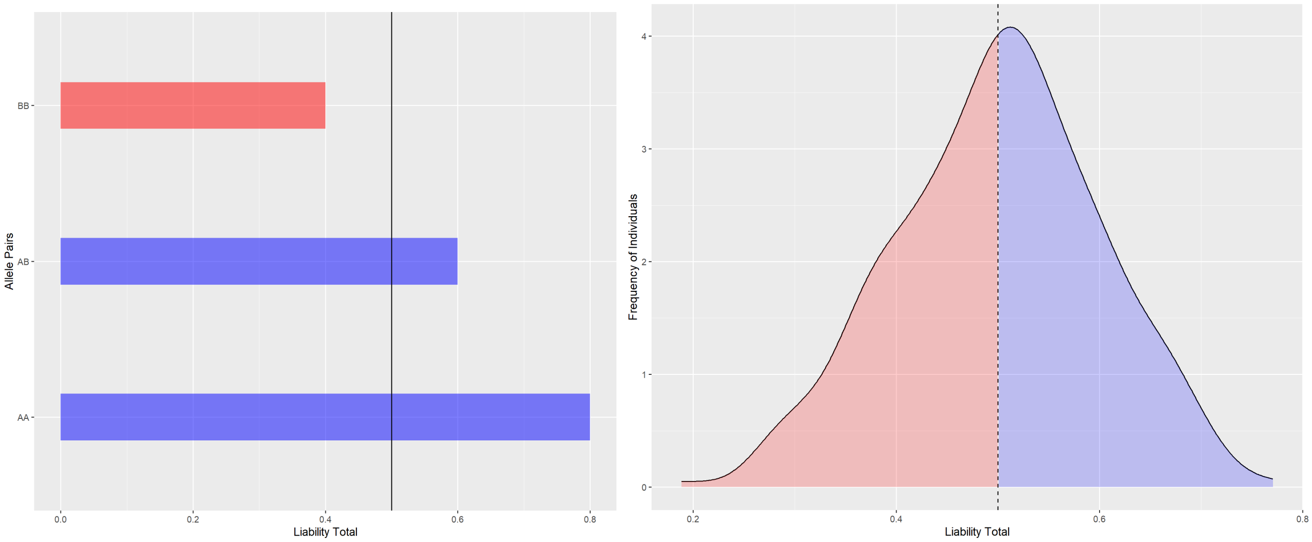
3.1.1 Liability Reaction norms

As mentioned earlier, not every behavioral or phenotypic trait can be described using a continuous linear frame work. Some traits manifest as discrete phenotypes or behaviors where there is an underlying, continuous liability, which produces one phenotype or the other depending on whether the liability exceeds a treshold or not. These liability values can consist of genetic factors, individual differences in environmental factors, a combination of both, or other unobserved factors. Traits that display different phenotypes based on a threshold that is passed are known as threshold traits. Examples of these threshold traits include making a decision to forage or stay in hiding based on perceived threat level (Turney and Godin 2014), when a crocodile hatchling's sex is determined by its incubation temperature (Hutton 1987), or in our case, whether to produce or scrounge. The liability to produce can be tracked using the same technique as the BRN and is called a Liability Reaction Norm (LRN).

In the following example, two populations of individuals are capable of displaying two color variants, red and blue. One has a color morph dependent on a single gene, while the other's depends on the combined effect of multiple genes. In the single locus example, displaying a certain phenotype depends on the additive property of the present alleles. In figure 3a, "B" alleles add a value of 0.2 to the liability total, "A" alleles add a value of 0.3 to the liability, and the threshold of displaying phenotype "Blue" is 0.5. Homozygous "B" individuals will display the "Red" phenotype as the total liability of 0.4 does not cross the threshold. Heterozygous and homozygous dominant individuals will both display the "Blue" phenotype as the respective liability totals of 0.6 and 0.8 cross the threshold. In the multi-locus example, the liability of displaying a certain phenotype depends on the additive property of multiple gene effects, i.e. a 'quantitative genetic' trait. By plotting the frequency distribution of the individuals and their total underlying liability levels in the population as shown in figure 3b, we can get a similar illustration of the threshold trait. Once again, individuals to the left of a threshold will display "Red" as their phenotype while those on the right display "Blue" as their phenotype.

LRNs can be "translated" into BRNs by taking the x-axis point or points at which that the LRN crosses the threshold and using it as the inflection point where the phenotype changes in the BRN. For a deterministic LRN, the corresponding BRN will be a step function, only giving probabilities 0 or 1 of expressing the alternative phenotypes. Using the previous example, say we have a population that has a liability threshold of 0 to display a blue phenotype that corresponds to a linear LRN as seen in figure 4a. The corresponding BRN seen in figure 4b would consist of a step function where an individual changes the displayed phenotype from 0% blue to 100% blue once the total additive value of the alleles surpasses 0.5.

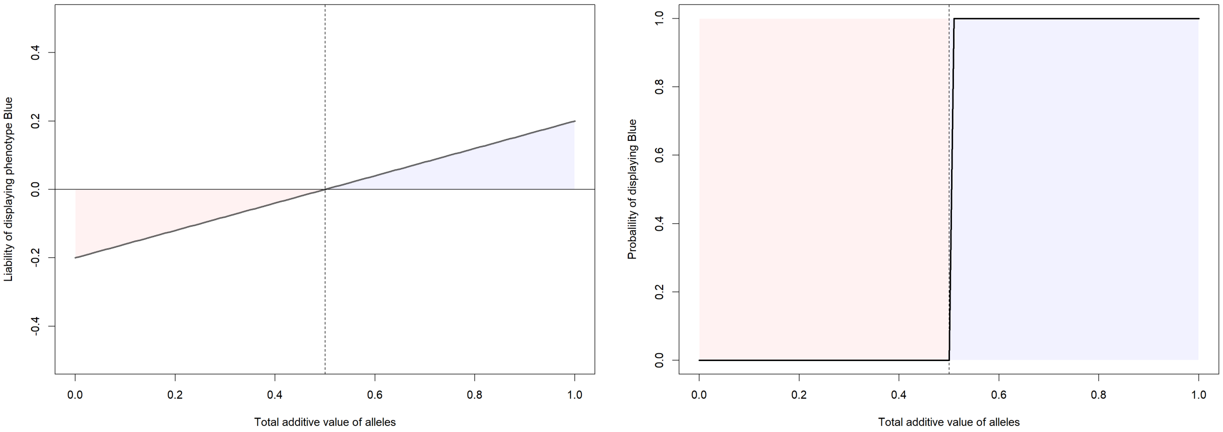
In these threshold traits, the LRNs can also differ in slope, elevation and shape, yielding different corresponding BRNs. Figure 5 shows five linear LRNs (left column) with differing elevations (top row) or differing slopes (bottom row) and their corresponding BRNs (right column). The LRNs in this example consist of environmental factors (social environment information) instead of the genetic factors of the previous example. In each line the individual does not display a producing phenotype in their BRN until the corresponding LRN line crosses the threshold. Moving from the dark green line to the dark red line in figures 5a and 5c, decreasing the elevation or slope of the LRN causes the LRN to cross the threshold at a higher information value. This causes the translated BRNs displayed in figures 5b and 5d to move their cross-over points correspondingly to display 100% producing at the value of social environment information where the LRN crosses the threshold. However, this example of



(a) Single Locus

(b) Multi Locus

Figure 3: Examples of two populations that use single and multi-locus genes to display red or blue color morphs with an underlying liability threshold of 0.5 that separate red and blue color morphs



(a) Liability Reaction norm

(b) Behavioral Reaction Norm

Figure 4: LRN and BRN of a population showing the transition of red and blue phenotypes

LRN depends on the assumption of perfect phenotypic precision and an environment devoid of noise.

Any reaction norm is subject to noise or variance and this can arise from a number of sources. It can arise from genetic components of the individual relative to the population, environmental conditions during development, differences in how individuals react to the same environmental stimuli, or some other unobserved factor (David F. Westneat et al. 2015). In addition, these components are both heritable by offspring and subject to evolutionary selection (Henriksen et al. 2020). When noise is present in LRNs, it typically arises from residual stochastic liability components that do not arise from genetic, environmental or plasticity variance. It further alters the shape of the corresponding BRN. Noise can "bump" a point on the LRN close to its threshold over, potentially causing an individual that displays one phenotype to display another. This makes it probabilistic whether the LRN crosses the threshold or not, creating a sigmoid BRN shape similar to the red line in 1f rather than the green step shape in the same figure. The amount of noise required to do so increases the further from the threshold the point on the LRN is.

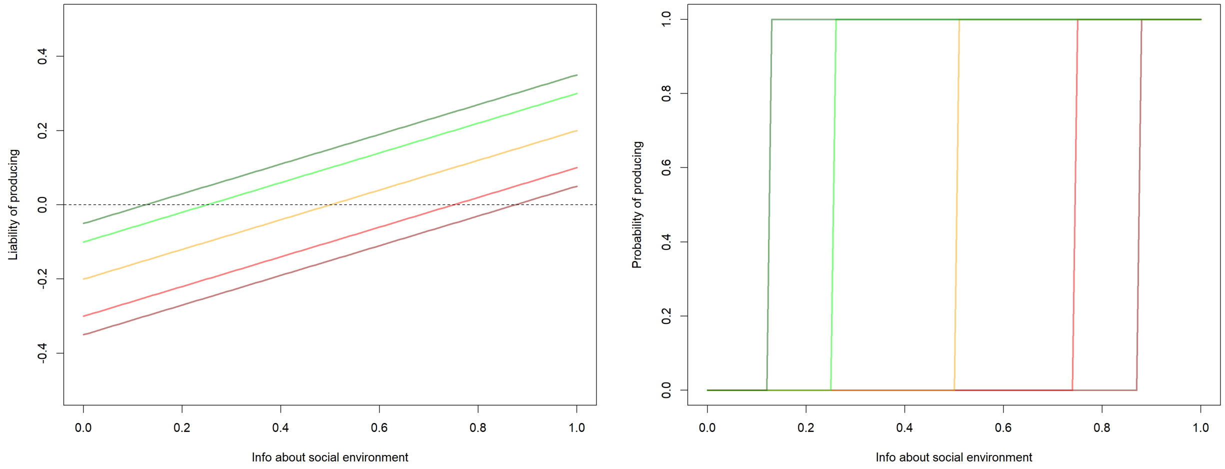
Figure 6 shows two sets of five linear LRNs (left column) with differing elevations (top row) or differing slopes (bottom row) and their corresponding BRNs (right column) in the presence of added noise. In the yellow line of 6a, the closer a point on the LRN is to the threshold of y=0 the greater the effect of noise is on the BRN point in figure 6b, causing the translated BRN point to be closer to y=0.5. At the furthest dark red LRN, no amount of noise can bring the LRN completly over the threshold enough to cause it to switch to 100% producing behaviour at any level of social information in the BRN. Similarly, in the dark green line no amount of noise can move the LRN point low enough to display 100% scrounging behavior.

When altering the slope of the LRN (bottom row of figure 6), moving from the dark green line to the dark red line, an increase in slope reduces the effect noise has on flattening the BRN. Thus a steep slope with environmental noise will look more similar to the step function seen in an example with no noise, while the dark green LRN with its shallow slope bringing all its points close to the threshold produces a near-linear BRN.

4 Aims

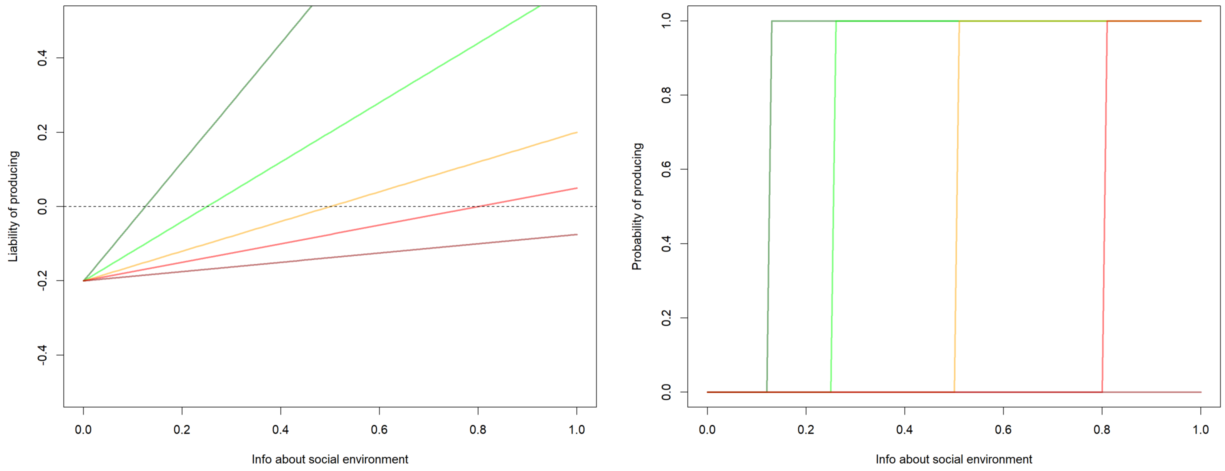
This model attempts to rectify shortcomings found in prior models.

- First, we aim to use an agent-based modelling approach to examine the evolution of individual strategies in a game theoretical context, going beyond ESS models only predicting population level frequencies of tactic use. We investigate how this depends on regimes of environmental variation changing the ESS, formulated as fluctuation in the producer bonus.



(a) LRNs with differing elevations

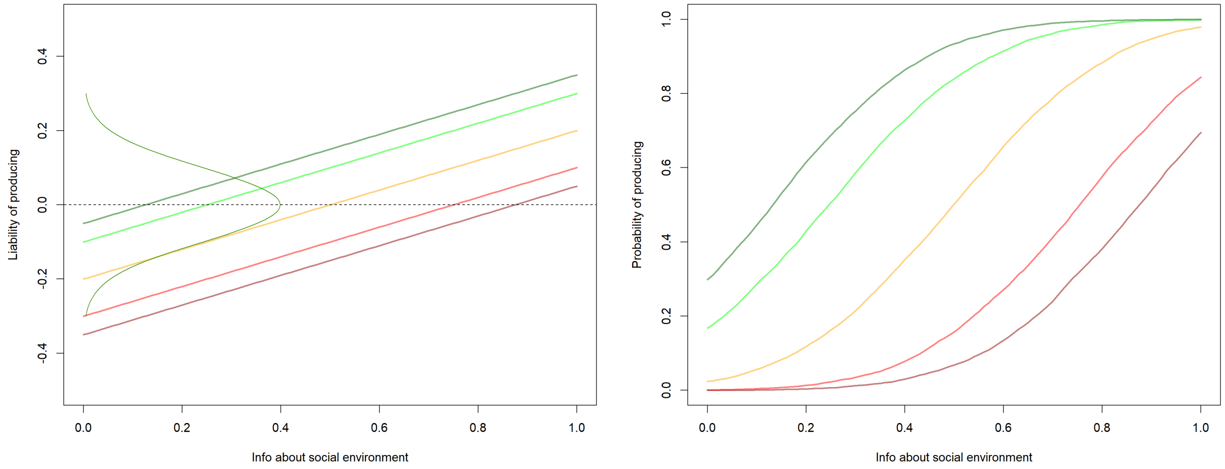
(b) Resulting BRNs from 5a



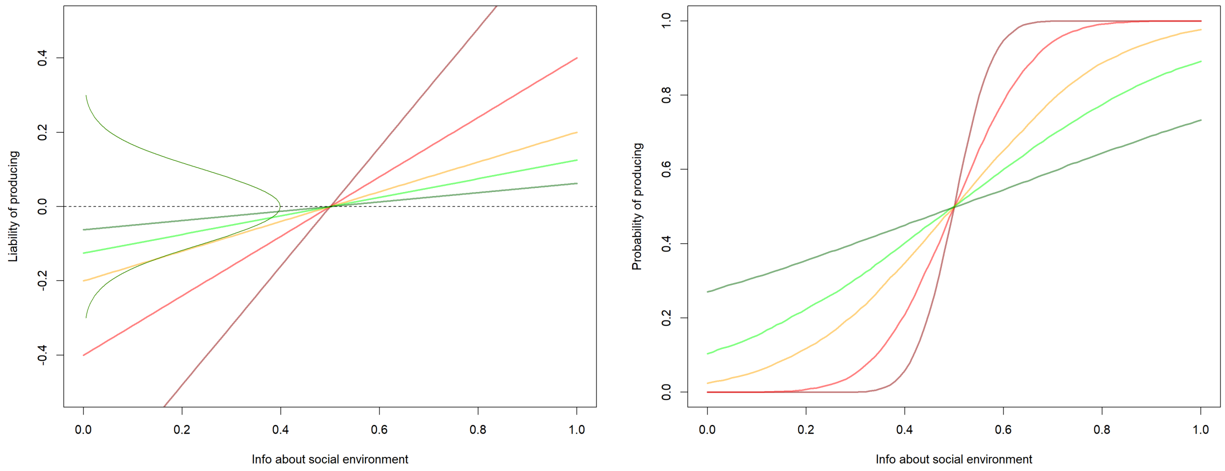
(c) LRNs with differing slopes

(d) Resulting BRNs from 5c

Figure 5: LRNs (left) of differing elevation (top row) and slope (bottom row) with their corresponding BRNs (right)



(a) LRNs with differing elevations with noise (b) Resulting BRNs from 6a



(c) LRNs with differing slopes with noise (d) Resulting BRNs from 6c

Figure 6: LRNs(left) of differing elevation (top row) and slope (bottom row) with their corresponding BRNs(right) in the presence of noise

- Second, I aim to address the shortcomings of Dubois, Morand-Ferron, et al. 2010 and Katsnelson, Motro, M. Feldman, et al. 2011. These models face a problem where they mix the concepts of non-plastic mixed strategies, conditional plastic strategies and plastic learning strategies as well as only comparing pure or non-plastic mixed strategies to a learning strategy. The "learners" in Dubois, Morand-Ferron, et al. 2010 are more akin to conditional plastic in their behavior, whereas the "learners" in Katsnelson, Motro, M. Feldman, et al. 2011, while behaving like learners, are not pitted against non learning plastic individuals. The model proposed will resolve this confusion by explicitly evolving learning(through memories of past experiences) alongside plastic, non-plastic-fixed and/or mixed strategies, distinctly defining each kind of strategy.
- Third, the addition of a liability framework transforms the decisions of probabilistically producing vs scrounging into a threshold trait. This allows for a flexible range of non-plastic (flat) and plastic (linear, sigmoid, step function) behavioral reaction norms to evolve through only evolving liability reaction norm elevation and slope (eq. 4).

4.1 Questions

Along with the above aims, we attempted to answer some direct questions with the model

- If plasticity (slope) is unable to evolve, when will populations consist of pure strategists at ESS frequencies, or mixed strategies playing each tactic in the ESS proportions, or intermediate combinations?
- If plasticity is allowed to evolve, what proportion of plastic as opposed to non-plastic strategists emerges under which conditions?
- If plasticity is allowed to evolve, what LRN elevations and slopes, and resulting BRN shapes, will emerge in the population?
- When will non-learning versus learning plastic strategies be favored?
- How does the range of variation in empirical observations of producer-scrounger game reaction norms evolve?

4.2 Hypothesis

There were a few hypotheses on the reaction of populations to the different types of environmental variation and variation speeds.

- The speed of the environmental change may affect the relative success of fixed vs mixed non-plastic strategies, plastic vs non-plastic strategies, and learning vs non-learning strategies.

  - Environments that change slowly would allow for individuals to easily follow the optimal ESS described in equation 3 closely and enable individuals to display more diverse types of behavior.
  - In environments that were too slow however, there would be little incentive for behaviors to evolve and change over time, as a behavioral type could work for many generations. Environments like these would probably see individuals gravitate towards fixed strategies as the slowly changing environment could more easily exploited at the maximum level.
  - In environments that changed quickly, it would be difficult for a population to follow the optimum ESS closly.
  - In environments that changed too quickly, there would also be little incentive for plastic behaviors to evolve as the environment would change before any one behavior could be successful for long. Environments like these would most likely be composed of individuals who would choose strategies that were good enough in most cases instead of attempting to perfectly track the conditions.

- Environments in the control scenario with no fluctuation between generations or within generations would most likely see very specialized, pure fixed strategies, with the possibility of mixed strategists, as the lack of change would allow for the optimum elevations to be quickly found, and once achieved, there would be no incentive to change, making costly plasticity highly unlikely to evolve. Memory would see no use as non-plastic strategies would not change the phenotype regardless of information held.

- Populations in environments that fluctuated within generations would include individuals that encounter variability in their own lives. For the population to survive, individuals would either need to display mixed behaviors that work decently in different conditions or evolve some plasticity to handle the change they experience in their life. Memory would have an important role for plastic learning individuals here to allow them to recall the past and inform their behavior. At a population level the average elevation would remain constant and plasticity would evolve, but at an individual level there would be both non-plastic mixed individuals at different elevations and plastic individuals.

  If enough individuals had strategies that supported eachother (enough individuals playing the producer tactic at a specific time to support themselves and the individuals playing the scrounger tactic) there is a possibility a pure strategist could live long enough to reproduce. Pure strategies could persist this way due to the average environment between generations being the same allowing an individual from one generation playing a pure strategy to have an equal chance of success as its predecessor, but they would be very rare.

- Environments that fluctuated between generations would have individuals that experience different conditions from their ancestors, but only one condition in their own lifetime. Pure strategists would do fine within their own lifetime, but their offspring would encounter a completely different environment that they would probably be unsuited for, leading to the death of the lineage. To ensure the survival of their progeny, individuals would need to evolve an even higher level of plasticity to allow their descendants to be able to succeed in the new environments they find themselves in.

  Alternatively, they could again evolve a more mixed strategy that would work in most environments instead of the ability to change their behavior to suit the environment. Memory might not be important in this scenario as the environment an individual experiences never changes. At a population level, plasticity and elevation could stay constant, with the individual variety translating into a consistent average. Another possibility is that both plasticity and elevation at population scale could fluctuate together, with a decrease in the ability to switch behaviors (plasticity) corresponding with an increase in utilizing a strategy that will do decently in different conditions.

- Environments that fluctuated between generations and within generations would produce the greatest amount of plasticity. Pure strategists would never survive without the highly unlikely chance the entire population changed to support the pure strategists generation after generation. Non-plastic mixed strategists, while being able to survive in this environment for a short time, would be out-competed by plastic individuals. Variability in elevation could still exist, but plasticity would be a constant both at the individual and population level.

5 Methods

5.1 Model

The model was based on the rate-maximisation producer-scrounger model proposed by (Vickery et al. 1991), where fitness increases linearly with food intake. Each simulation represents a foraging game where N haploid, asexually reproducing individuals compete for food, distributed in patches, in a changing environment. These individuals play the producer-scrounger game and reproduce for a set number of generations. Each generation lasts a set amount of steps. At the end of the set number of timesteps, the generation ends, and individual selection for fitness and reproduction occurs. All individuals are removed at the end of the generation and replaced with the offspring of those that met the selection criteria. In this way, the population size remains constant and there are no overlapping generations.

Each timestep consists of a round of the producer scrounger game. At the beginning of each timestep the individual is able to choose between searching for food ("producing"), or joining others that have already found food ("scrounging"). If the individual chooses to produce, it has a set chance p of finding a food patch, consisting of F food items. If food is found, the producing individual enjoys a set amount of a food items a_{fs} (the "producer advantage", or finder's bonus) before any scrounging individuals are able to arrive. If the individual chooses to scrounge, it will equally divide the remaining F-a food items of a patch with the producer and all other scroungers. The assumption made is that scroungers are not limited to a single food patch, but are able to scavenge from any and all producers. Violation of this assumption alters the exact ESS frequency of scroungers (Ohtsuka and Toquenaga 2009, Dubois and Richard-Dionne 2020, Tóth et al. 2009, McNamara and Leimar 2020), but does not change the fundamental frequency-dependent aspect of the game.

For producers, expected food intake per time step is thus

$$I_p = a_{fs} + (f - a_{fs})/(1 + S) \tag{1}$$

where S is the number of individuals scrounging in that time step. Scrounger payoff is

$$I_s = a_{fs} + (f - a_{fs})/(1 + S) \tag{2}$$

provided that at least one producer finds food. If not, I_s=0. The expected ESS under such a game is

$$ESS = a_{fs}/f + 1/N \tag{3}$$

where N is total population size.

The model was developed in Rstudio and to visualize results, the packages ggplot, MASS, RColorBrewer and vioplot were used. Parameters and values used in the simulation are listed in table 3 below.

5.2 Selection and Reproduction

As the individuals in the model asexually reproduce, it is impossible for them to not find a mate. Instead of sexual success, this model utilizes food intake as its selection criteria. When a population reaches the end of a generation, individuals that have either not found food, have used more energy than the food can replenish, or have too high of a cost from their gene values will have an intake value<0 and die off. This new population is further diminished by truncation selection, eliminating all individuals in the lowest quartile of food intake. The final remaining population is weighted by their final food intake. The higher weight individuals are more likely to be chosen to reproduce. When individuals reproduce, their offspring inherit their genetic profile and strategies, except when mutations occur (see below).

5.3 Gene Evolution

For each round and generation four genes were tracked in this model, Elevation, Slope, Memory, and Information. The four genes together are used to calculate the liability of producing and the weight the individual gives information.

5.3.1 Calculation of Liability

The choice of producing or scrounging was treated as a threshold trait, such that whether or not the underlying liability y exceeds the threshold of y=0 dictates the expression of either tactic(Reid and Acker 2022). Individuals whose liabilities fell below 0 were displaying the scrounging tactic and individuals with a liability above 0 were displaying the producing tactic. The liability of producing for an individual i at time step t is given by

$$y_{i,t} = a_i + b_i x_{i,t} + c_i \varepsilon_{i,t} \tag{4}$$

where a is the elevation gene value, b is the value of the slope gene, and x is the value of the individual's information about its social environment. ϵ represents residual, irreducible noise from undefined sources, and has Gaussian distribution of mean 0 and standard deviation 1. The constant c is set to 1, scaling the effect of noise.

5.3.2 Information and Memory

In this model two different sources of information about the social environment are available to individual, public and private information. Their information gene determines which of the information types an individual uses to inform its decisions. Private information compares the payoffs of producing versus scrounging,

$$\mu_{priv} = \frac{V_p}{V_p + V_s} \tag{5}$$

where V_p and V_s are the payoffs of respectively producing and scrounging, such that higher values indicate that producing is better relative to scrounging. Each time and individual produces or scrounges its stored V_p and V_s values are updated.

Public information surveys the tactic use in the population,

$$\mu_{pub} = \frac{S}{P + S} \tag{6}$$

where P=N-S is the number of producers in the population, such that higher values indicate that there are more scroungers in the environment, again causing higher values to indicate that producing is better relative to scrounging. The information gene has only two alleles (0/1), where individuals observing the amount of scroungers in the population had a value of 0, and individuals using the payoffs of tactics had an info gene value of 1.

Furthermore, plastic individuals can utilize memory of prior information to weigh decisions and update their information over time ("learning"). Information was updated using the Rescorla-Wagner learning rule using equation (Afshar and Luc-Alain Giraldeau 2014),

$$x_{i,t} = x_{i,t-1} m_{i,t} + x^{'}(1 - m_i) \tag{7}$$

with m representing the weight of information from previous timesteps x, and (1-m) representing the weight given to newly acquired information x'. Thus, the individual's perception of its environment depends on its current and/or past public or private information

We utilized a memory cutoff value of 0.01 to classify individual using a learning strategy. A value >0.01 represents an individual that is able to learn while a value of <0.01 represents a non-learning individual.

5.3.3 Mutations

Mutations occur at the end of each generation with a probability determined by the mutation rate. When a mutation occurs for the slope, elevation and memory continuous genes, a new value is given to the offspring based on a Gaussian distribution around the parents gene value, with a standard deviation equal to the mutation size incrementally changing it over generations. As the info gene is binary and not continuous, when a mutation occurs the offspring's gene simply alternates between the values of 1 and 0.

5.3.4 Costs

We assume that the memory and plasticity genes are able to impose a cost to the fitness of an individual. If the benefit of a higher gene level to an individuals fitness outweighs its cost, the individual will tolerate the cost in order to receive the advantage that higher gene value might have. Costs imposed by genes were represented by reducing food intake linearly with increasing gene values,

$$I_i = I_{i,u} \times (1 - \alpha_{cost} \times |\alpha|) \tag{8}$$

where I_i is the modified intake of individual i, $I_{i,u}$ the unmodified intake, α_{cost} the cost imposed by gene α (plasticity or memory). No costs were implemented for the elevation or info type genes.

5.4 Tactics

5.4.1 Strategy Types

We defined 4 distinct strategy types that individuals could display. These definitions were applied to individuals after the genes had been allowed to evolve freely throughout the game. Figure 7 represents a decision tree of these strategies.

- The pure fixed strategy is a strategy that plays one tactic 100% of the time in all environmental conditions. We classified individuals as using pure fixed strategies if they had slope genes with an absolute value of <0.01 and an elevation gene with a absolute value >5. This large elevation value ensures that with the chosen size of environmental noise (c=1), the opposite phenotype is never chosen. This strategy looks like a more extreme version of the green and red examples in 1c.
- The non-plastic mixed strategies are strategies that play multiple tactics at different probabilities. These probabilities do not change based on the environment. We classified individuals as mixed strategies if they had slope genes with an absolute value of

Variable Name	**Variable Symbol**
ESS	ESS proportion of producers
a_{fs}	Producers bonus or "finders share"
f	Food items in a food patch
N	# of individuals in the population
I_s	Produced food at time step s
a_s	Producers bonus at time step s
S	# of scroungers exploiting the producer
y	Liability to produce
$y_{i,t}$	Liability of producing for an individual i at time t
a	Elevation
b	Slope
x	Value of the information gathered by the individual
c	Noise of an individual related to within-genotype and within-individual variance(in this model c=1)
ε	Residual noise
V_p	Payoff of the producing tactic
V_s	Payoff of the scrounger tactic
$\#_P$	# of producers
$\#_S$	# of scroungers
$x_{i,t}$	Information value at time t for individual i
m_i	Value of the memory gene of individual i
$1 - m_i$	Weight given to new information gathered by individual i
$x^{'}$	Past information gathered
I	Individuals food intake after application of genetic costs
I_i	Unmodified food intake
α	Gene value
α_{cost}	Cost imposed by gene α
$\bar{x}$	Mean value sin wave was centered on
A	Amplitude
G_s	Time step in a generation
T	Period
v	Frequency or cycles
S	The number of timesteps in a generation

Table 2: Variables and symbols in equations

Varible Name	**Variable Symbol**	**Value**
Replicate simulations	Rounds	20
Adult population size	N	50
Timesteps per generation	S	50
Number of generations	G	2000 for "Nofluct","Intragen" and "Intergen".
		5000 for “Both”
Food items per patch	F	20
Producers advantage	A	9
Probability of finding food while producing	P	0.25
Mutation rate	Mrate	0.1(Elevation),0.25(Slope)
		0.1(Memory),0.1(Information type),0.1
How many sine waves the fluctuations make through the given number of time steps (specific for generations)	Cycles_gen	1
How many sine waves the fluctuations make through the given number of time steps (specific for timesteps)	Cycles_step	1
How long a wave should be in timesteps (specific for generations)	period_gen	Slow: 2000 Medium: 200 Fast: 20
How long a wave should be in timesteps (specific for timesteps)	period_step	Slow: 50 Medium: 50 Fast: 50
How high a wave should be (specific for generations)	Amplitude_gen	3
How high a wave should be (specific for timesteps)	Amplitude_step	1
Elevation sine waves will be symmetrical (specific for generations)	Mean_gen	0
Elevation sine waves will be symmetrical (specific for timesteps)	Mean_step	0
Mutational effect size	msize	0.1
Cost of being plastic (fraction of intake) Scales with LRN Slope gene	pcost	0.01
Cost of using memory (fraction of intake)Scales with memory gene	mcost	0
Cost of switching tactic (fraction of intake)	scost	0
Truncation selection	sel_trunc	0.25
Producers bonus fluctuation type	prodbonus_fluct	“none”,””"Intragen"”,””"Intergen"”,””"Both"”

Table 3: Parameters and values used in simulation

<0.01 and an elevation gene with a absolute value <5. These strategies reaction norms look like the orange example in figure 1c.

- Plastic strategies were classified as Adaptive or Mal-Adaptive depending on the sign of their BRN slope. Adaptive strategies had slopes >0.01 and increased the probability of producing as information values increased and Maladaptive strategies had slopes < -0.01 and decreased their probability in the same conditions. These plastic strategies were also further broken into the following strategies:
- Step conditional strategies had behavioral reaction norms that formed a step function as seen in the green example in 1f. These individuals are characterized by their high slope gene with an absolute value >6.5. These strategies were further split by which information type they used. Those who use payoffs had an Info gene of 1, while those that used the %scrounger in a population had a value of 0.
- Log conditional strategies had behavioral reaction norms that formed a sigmoid function similar to the red example in 1f. These individuals are characterized by their lower slope gene with an absolute value <6.5 and >0.01. These strategies were further split by which information type they used. Those who use payoffs had an Info gene of 1, while those that used the %scrounger in a population had a value of 0.
- The Learning strategies had slope genes with an absolute value >0.01 and a memory gene with an absolute value >0.01. These strategies were further split by which information type they used. Those who use payoffs had an Info gene of 1, while those that used the %scrounger in a population had a value of 0.

5.4.2 Individual Variation

Population level ESSs do not always portray accurately what occurs at the individual level. It is possible for a population to display a phenotype while the individuals in the population do not display the same phenotype(Maynard Smith 1974). For example the population strategy could be mixed 50% producing and scrounging while individuals are a combination of pure 100% scrounging or 100% pure producing strategies. Alternatively the same population ESS could be achieved by individuals playing a pure 50/50 producer scrounger strategy For 10 of the replicates that were run the reaction norms of 20 random individuals in the population were isolated at the final timesteps and plotted by the information (Payoffs or %producers) and the probability to produce (y-axis). This was done in order to observe the differences between the ESS strategy of the population and what strategies were actually being utilized by individuals.

5.5 Environmental variation

Previously, this particular model utilized an auto-correlation function to manage variability in the environment by creating variability in food intake (Bharath 2023). While the

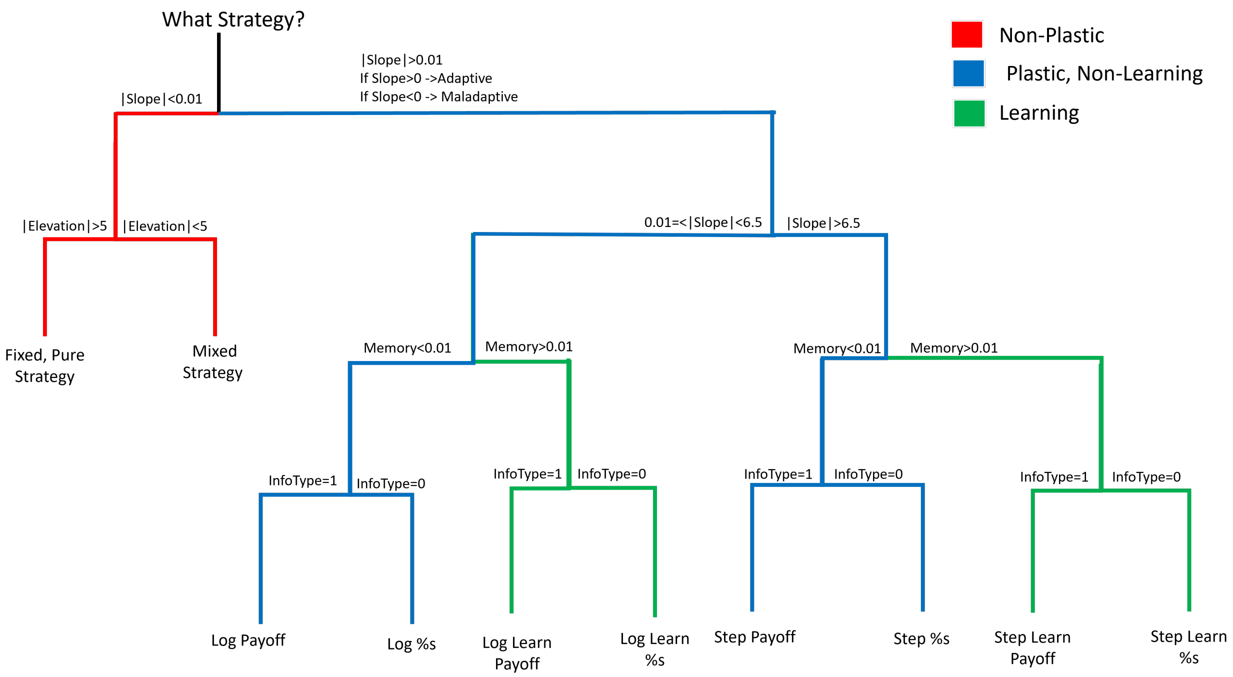


Figure 7: Strategy tree detailing the possible strategies found in the model

autocorrelation produced a varied environment, it was difficult to predict. In contrast, in this model the producers bonus a_{fs} was altered to change the benefit of producing for a corresponding generation or timestep using a predictable deterministic correlation through a sinusodial function. By altering the producers bonus, the ESS fraction of producers and scroungers would also change. This was done to create a changing, but more predictable environment than using an autocorrelation function.

In order to vary the environment across time a deterministic function was used that produced a sine wave of a length equal to the total number of generations with a period divisible by the number of timesteps in a generation. This sine wave was then centered around a mean of zero to ensure the wave would be centered around the long-term mean. The resulting y value on any point in the sine wave could then be used to modify the environment through any selected variable. This environmental variability can be set to act each generation, each timestep within generations, or both, and intra- or intergenerational variability can be independently modified. The following sinusoidal function was used to generate environmental variation,

$$y = \bar{x} + (A \times sin(G \times 2\pi/T) \tag{9}$$

where x̄ represents the mean the wave was centered on, A represents amplitude, G represents a generation, T represents the period.

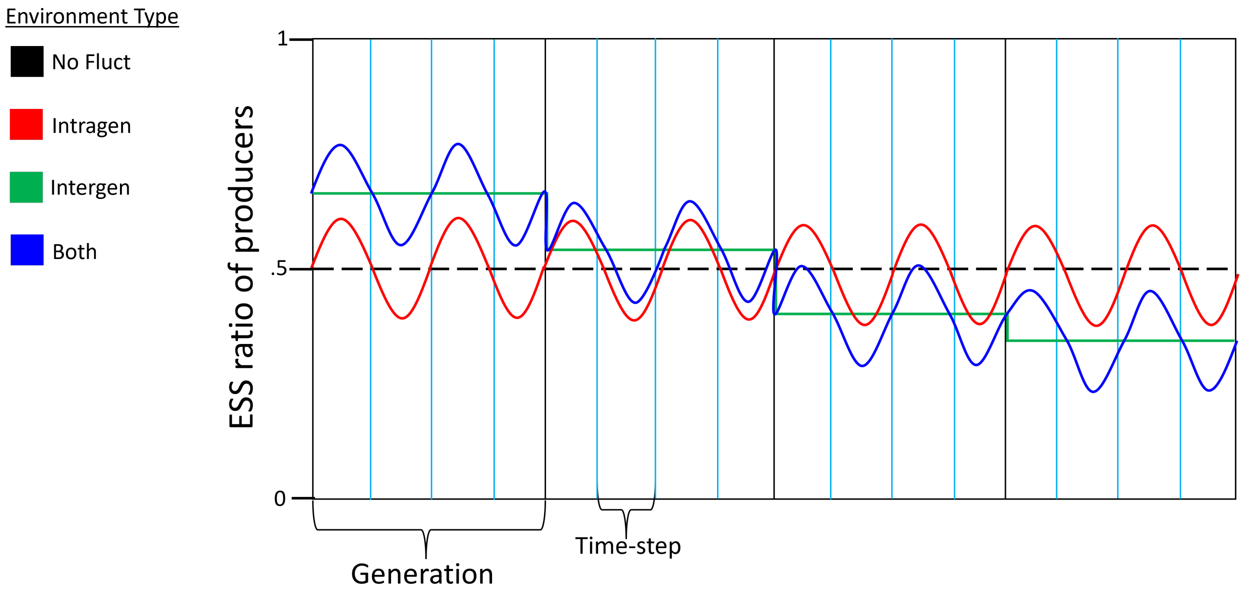


Figure 8: Different types of environmental fluctuation with the environment changing within generations(red), between generations(green) or both(blue)

5.6 Types of Environmental Fluctuations

4 types of environmental fluctuation were tested with this model. Each scenario differed in how the producers bonus and the optimal ESS changed over time and is shown in figure 8.

- The "NoFluct" scenario was a control scenario where no environmental variation occurred either between or within generations.
- The "Intragen" scenario involved an environment that changed only within generations.
- The "Intergen" scenario involved an environment that changed only between generations.
- The "Both" scenario involved an environment that changed both between and within generations

Non-plastic Scenarios

In order to have a control scenario for plasticity, 3 non-plastic scenarios were run to both observe changes occurring through cycle speed and fluctuation types. The slow scenarios involved an environment that changed slowly with a complete cycle taking 2000 generations. Medium scenarios involved an environment that changed with a complete cycle taking 200 generations and fast scenarios involved an environment that changed very fast with a complete cycle taking only 20 generations. Any changes in plasticity and memory in comparison to the plastic scenarios would be a result of the slope and memory gene, the mutation size and the cost of plasticity and memory. For the non-plastic scenarios, the slope mutation rate was set to a value of 0 and the memory gene had a value of 0.1, and neither gene had a cost.

Plastic scenarios

The plastic scenario was run with an increased slope mutation rate and a cost to plasticity and memory of 0.02. The environmental fluctuation speed was identical to the medium scenario. All other parameters were identical.

6 Results

6.1 Non-Plastic scenarios

Non-plastic scenarios were characterized through the inability of plasticity to evolve. The main variation in non plastic individuals was unsurprisingly the elevation gene. This variation in elevation would show which tactic a mixed individual would be more inclined to use. A mixed individual could play more producer tactics than scrounger, more scrounger than producer, or it could have a strategy closer to 50/50 of each tactic.

In figure 9 the values of the slope, elevation and memory are shown for different environmental fluctuation types and speeds. Values were taken from the final 500 generations of the simulation and can be found in table 4. Medium and fast environments gave similar results to each other as seen in figures 9b and 9c. Notably, when environments change sufficiently quickly between generations (medium and fast "Intragen" and "Both" scenarios), the variation in the elevation gene is much smaller than otherwise (see also 11).

In most non-plastic scenarios, the mean elevation gene was negative, indicating that individuals would be slightly more inclined to scrounge, capturing the long-term ESS of approximately 45% producing. However, in the slowly changing environment, averaging over the last 500 years of the simulation captures only the part of the environmental sine wave where the producer bonus is higher than the long-term average, favoring more producing and causing positive elevations. Similar patterns were seen for the "Intergen" and "Both" scenarios. In all cases, the memory gene is selectively neutral (since there is no benefit and no cost) and so it drifts around 0.5.

The ESS proportion of producers was also affected by the speed of environmental fluctuation and became more difficult to follow for the population as the conditions of the environment became faster and began to change between generations, with the population completely unable to follow in a fast environment that changed between generations. The effect of environmental speed can be seen in figure 10. At lower speeds, populations were able to follow the optimum ESS with some lag. At high speeds however, these environments showed ratios of producers and scroungers more similar to environments that only changed within generations, as the population could not begin to follow the ESS.

Figure 11 shows some strategies (reaction norms) used by individuals in a non-plastic, medium speed environment. Non plastic scenarios were dominated by mixed strategists, with pure strategies only seen in a few individual reaction norms at medium "Nofluct" and slow "Intergen" environmental conditions. For most environmental conditions, mixed strategies were the only strategies in the population. Figure 11 also shows that as the environment begins to change between generations, the elevations of individuals begin to condense and are on average closer to the ESS (0.45) than in environments that do not change or only change within generations.

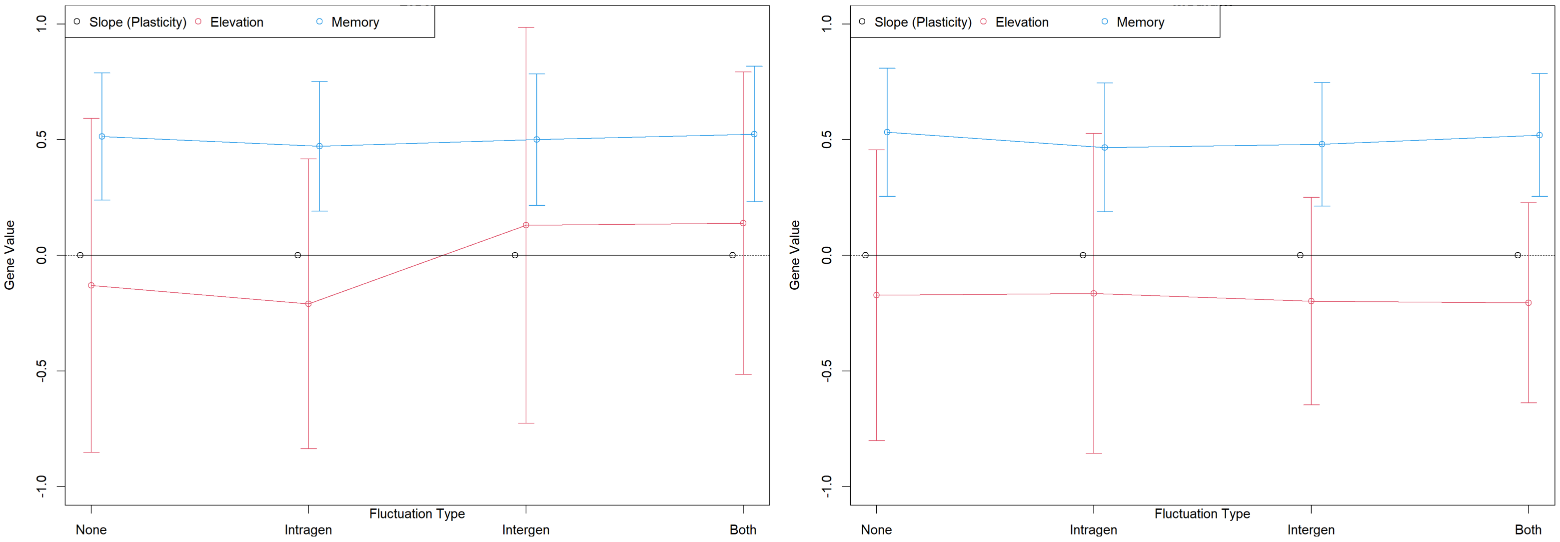
6.2 Plastic scenario

The plastic scenario was run with the same speed of environmental fluctuation as the medium non-plastic scenario. Unlike the non-plastic examples, there were costs to the evolution of the slope and memory gene. In the plastic non-fluctuating environment in figure 12 the mean values of all genes were closer to zero. The standard deviations were also lower than those seen in the non-plastic scenarios, most likely due to the gene costs. In scenarios with environmental variation, the elevation and slope gene both diverge from a zero value. The slope gene increases and the elevation gene decreases. The memory gene stays relatively stable, with the mean increasing slightly. Elevation and slope would reach their furthest separation when environments fluctuated between generations only, and move towards each-other again when the environment changed both between and within generations. The memory gene would have its largest increase in this environment type. Figure 13 details how these genes evolved in the plastic scenario over time and shows this same pattern. This shows how elevations and slopes tend to covary over time, where the population tracks the fluctuating ESS by either using positive higher elevations and high plasticity, or lower elevations and less plasticity.

Figure 14 shows the classification of strategies found in the different plastic scenarios. Learning strategies were the most common strategy type in the plastic scenario, given the high evolved memory factors. Non-learning plastic strategies were less common, and non-plastic mixed strategies were very rare. In both learning and non-learning plastic strategies, there were equal numbers of individuals utilizing the %producer as information as the payoffs.

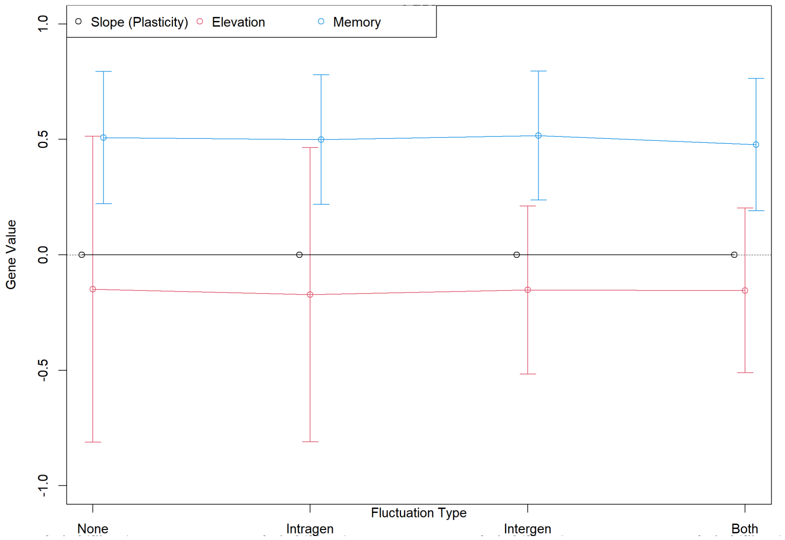
7 Discussion

Our model set out to address the short-comings of prior models and provide a more informative picture of the evolution of various strategies in the producer scrounger game and how they are impacted by a changing environment. We were able to observe the success of



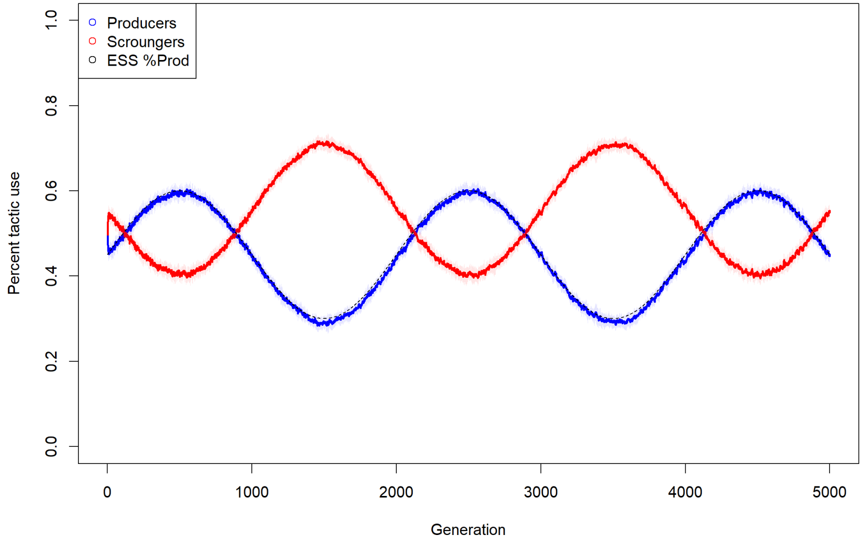
(a) Slow

(b) Medium

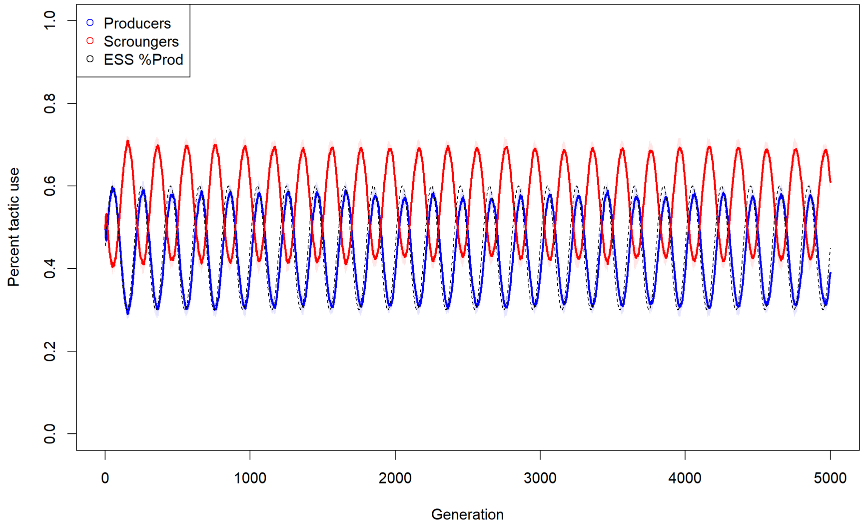


(c) Fast

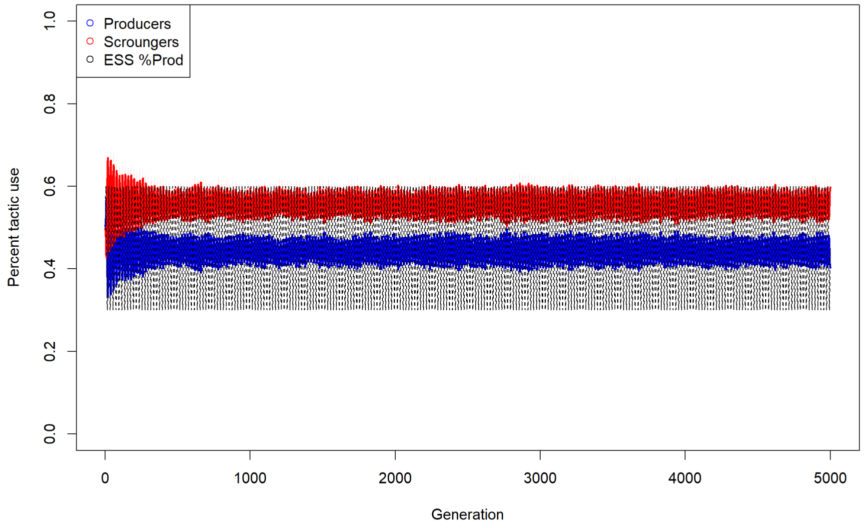
Figure 9: Scaleplots of non-plastic scenarios



(a) Slow

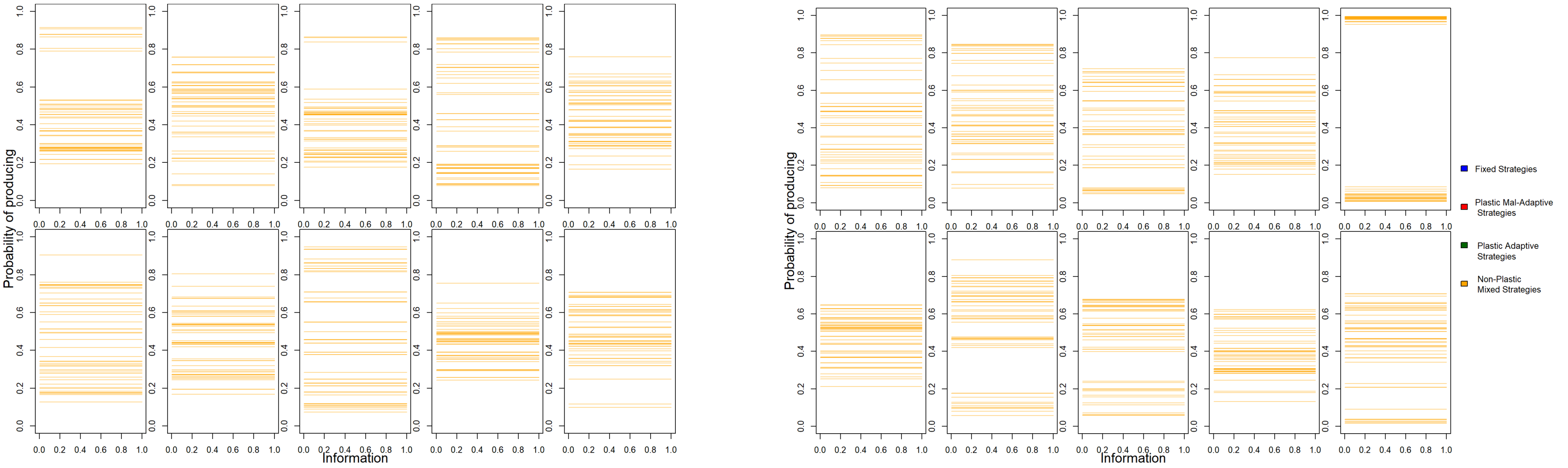


(b) Medium



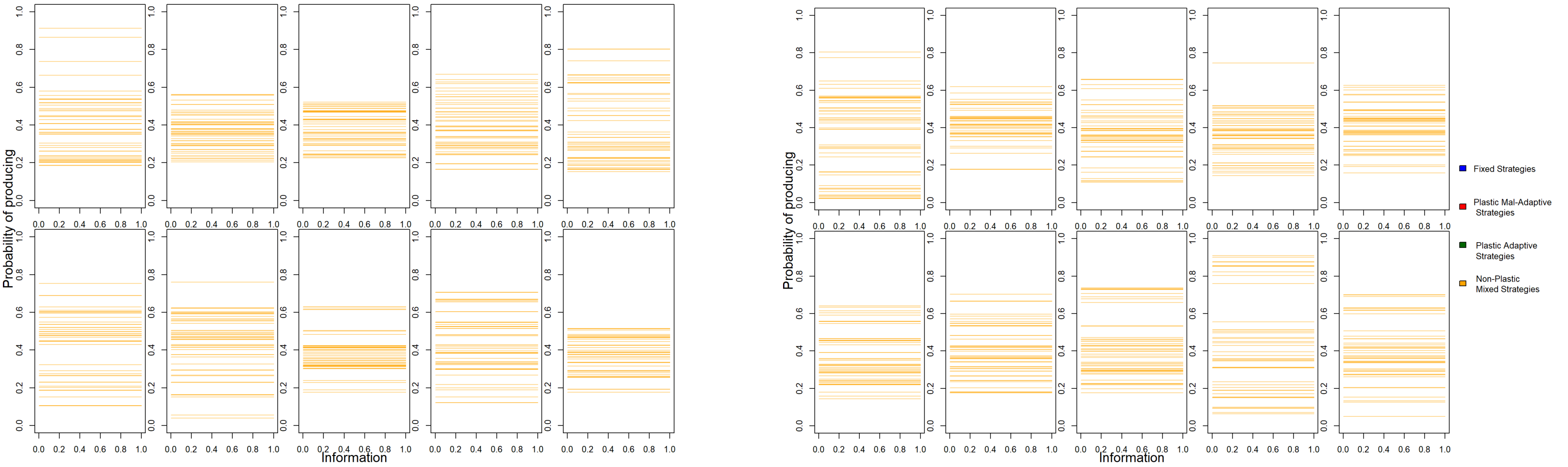
(c) Fast

Figure 10: Producer/Scrounger ratio plots of slow, medium and fast non-plastic scenarios in environments that fluctuate within and between generations. Increasing speed causes the population to struggle to follow the ESS



(a) NoFluct

(b) Intragen



(c) Intergen

(d) Both

Figure 11: Individual strategies found in the medium non-plastic scenario. Information on the x-axis refers to the combination of information about the payoffs of strategies and the %scroungers in the population. Environments that do not change between generations(11a,11b) show a larger range of elevation values, while environments that change between generations(11c,11d) have a more condensed range.

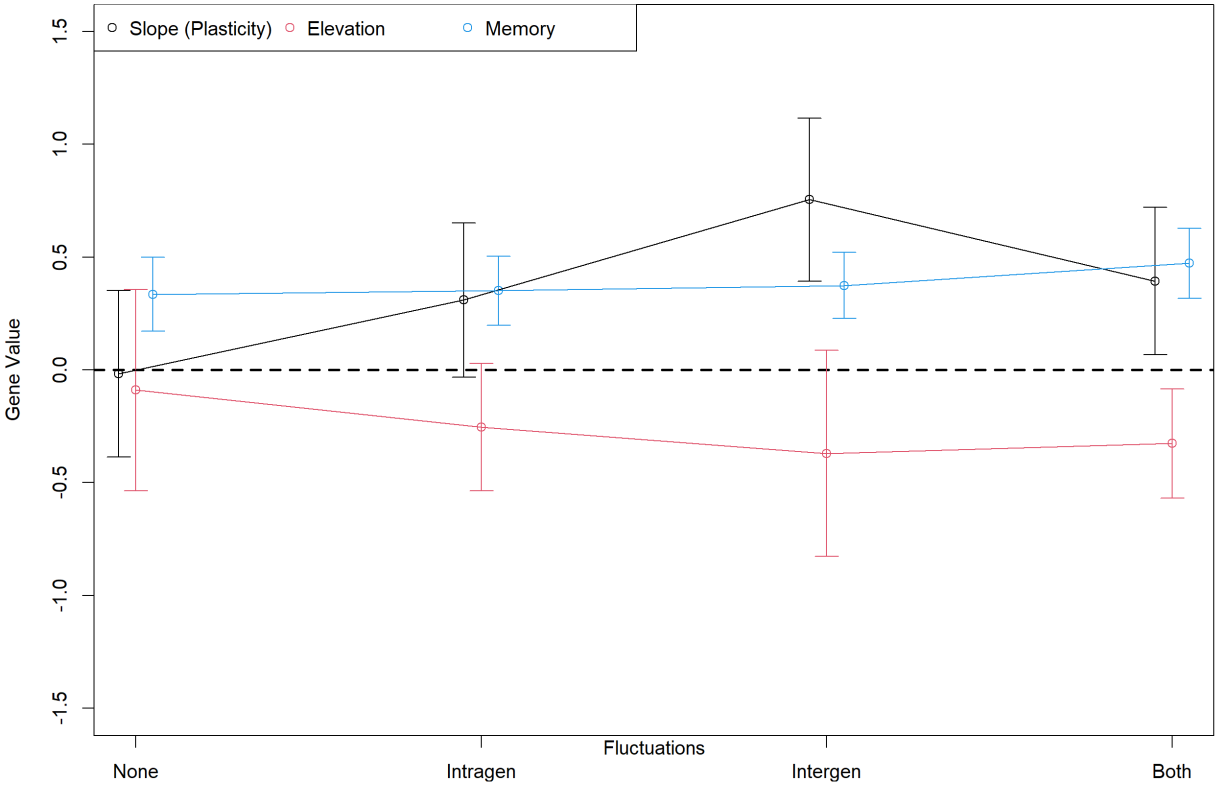
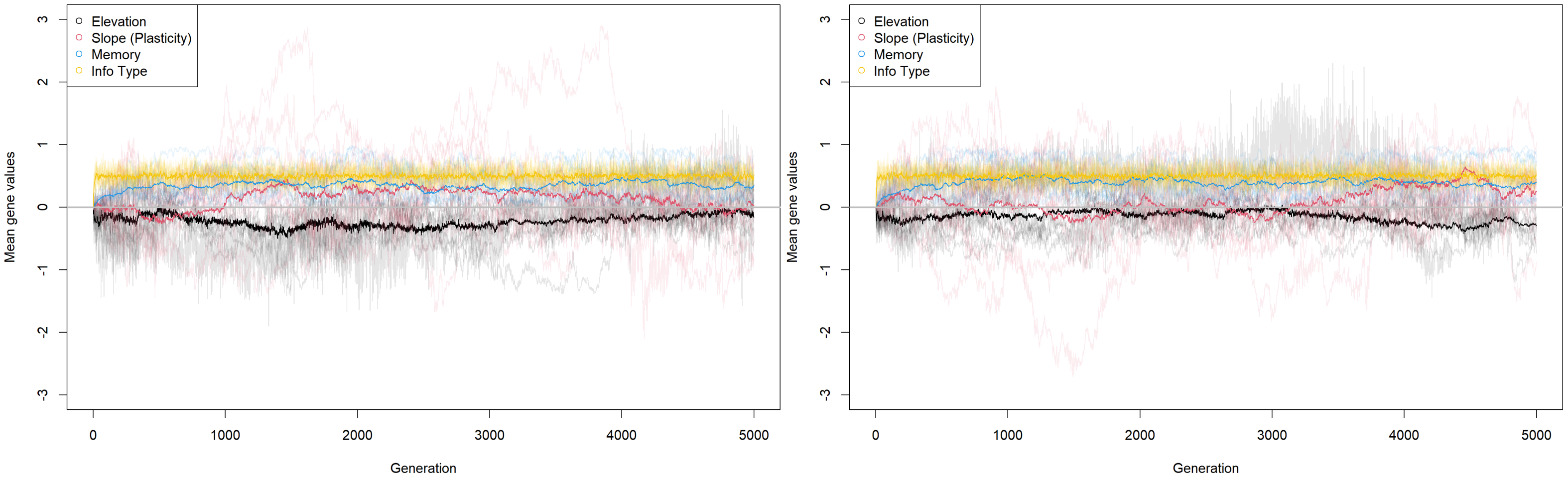
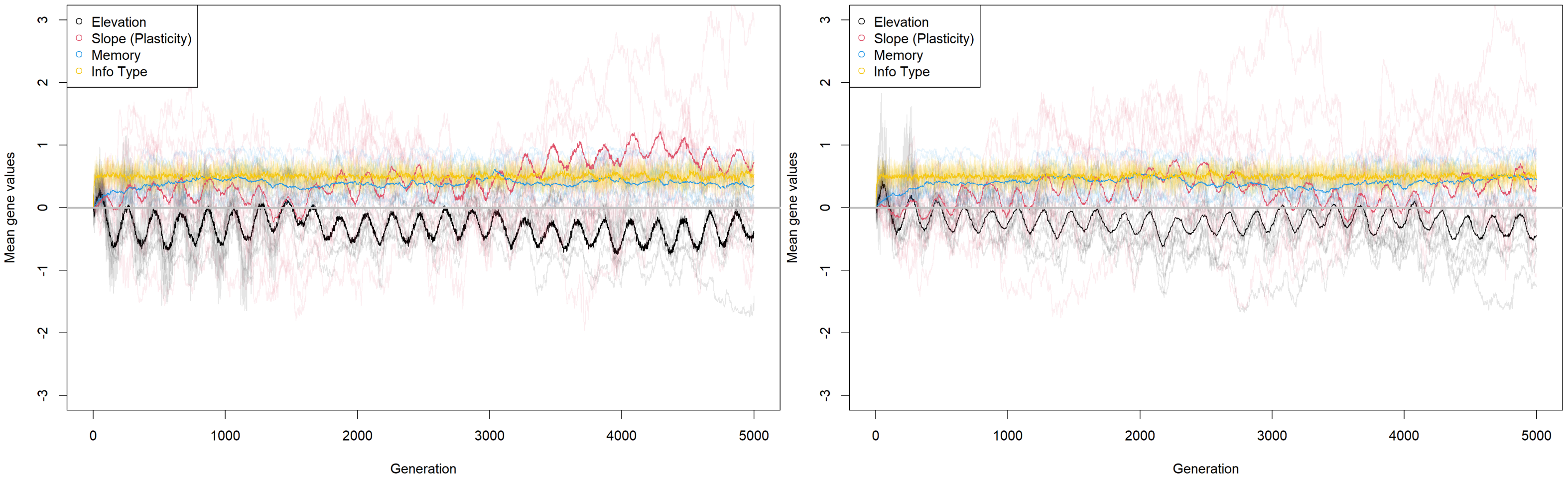


Figure 12: Scaleplot of plastic scenarios



(a) NoFluct

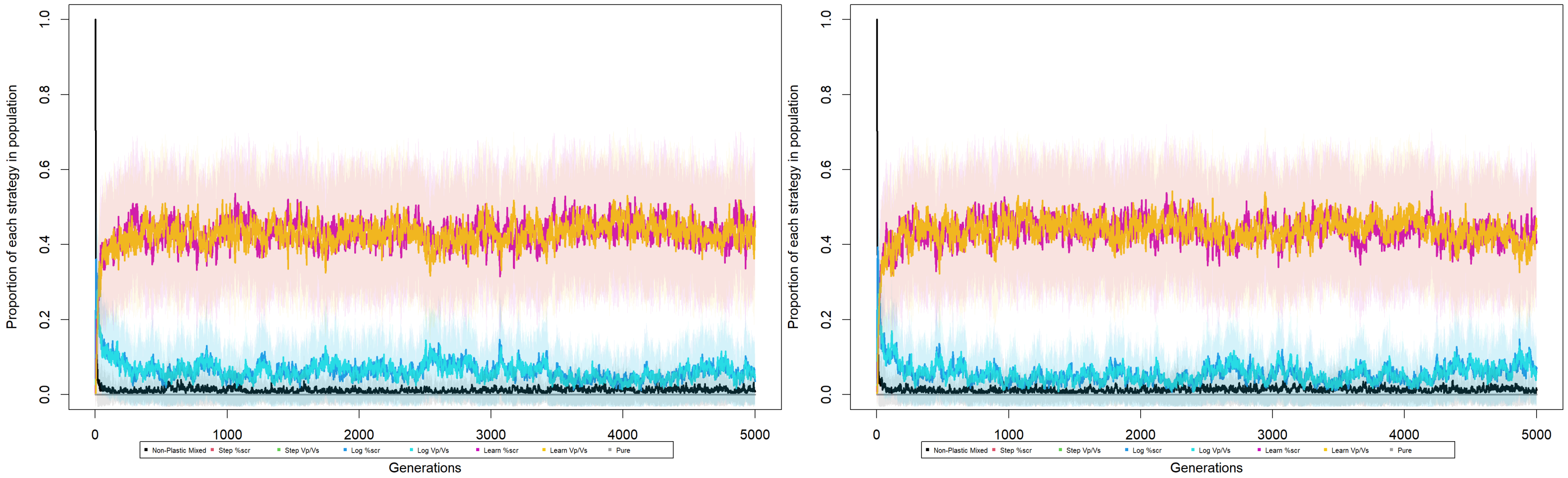
(b) Intragen



(c) Intergen

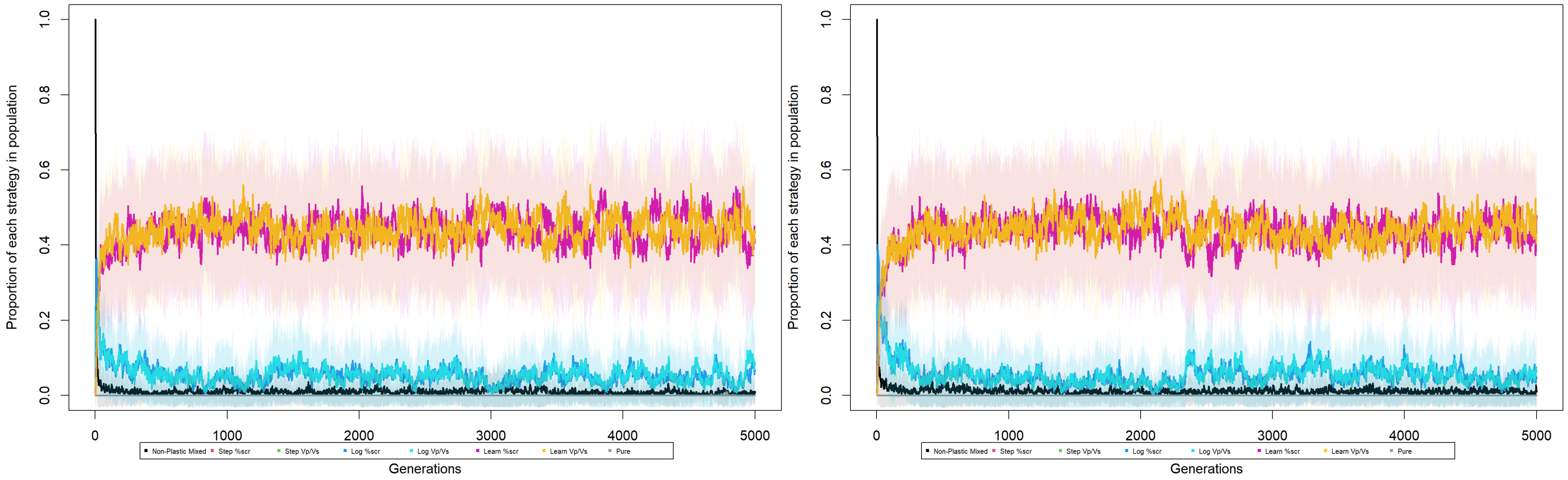
(d) Both

Figure 13: Gene-plots of plastic scenarios with slope and elevation showing an inverse frequency relationship



(a) NoFluct

(b) Intragen



(c) Intergen

(d) Both

Figure 14: Strategies found in plastic scenarios. Learning plastic strategies in orange and pink were the most numerous across all plastic scenarios. Non-learning plastic in dark and light blue was the second most numerous, followed by non-plastic mixed in black

Environmental conditions	**Mean *a***	**SD *a***	**Mean *b***	**SD *b***	**Mean *m***	**SD *m***
Non-Plastic-Slow-No Fluct	-0.130	0.722	0.000	0.000	0.514	0.275
Non-Plastic-Slow-Intragen	-0.210	0.626	0.000	0.000	0.471	0.280
Non-Plastic-Slow-Intergen	0.130	0.856	0.000	0.000	0.500	0.284
Non-Plastic-Slow-Both	0.139	0.654	0.000	0.000	0.524	0.293
Non-Plastic-Medium-No Fluct	-0.173	0.629	0.000	0.000	0.532	0.277
Non-Plastic-Medium-Intragen	-0.165	0.692	0.000	0.000	0.466	0.279
Non-Plastic-Medium-Intergen	-0.198	0.448	0.000	0.000	0.480	0.268
Non-Plastic-Medium-Both	-0.205	0.433	0.000	0.000	0.520	0.266
Non-Plastic-Fast-No Fluct	-0.149	0.663	0.000	0.000	0.508	0.286
Non-Plastic-Fast-Intragen	-0.172	0.637	0.000	0.000	0.499	0.280
Non-Plastic-Fast-Intergen	-0.152	0.364	0.000	0.000	0.516	0.279
Non-Plastic-Fast-Both	-0.154	0.357	0.000	0.000	0.477	0.286
Plastic-No Fluct	-0.090	0.446	-0.017	0.369	0.335	0.163
Plastic-Intragen	-0.254	0.282	0.309	0.342	0.351	0.153
Plastic-Intergen	-0.370	0.458	0.755	0.362	0.374	0.146
Plastic-Both	-0.326	0.242	0.394	0.327	0.472	0.155

Table 4: Means and Standard deviations of genes taken from the final 500 generations.Displayed in graphical form in figures 9 and 12. a=elevation gene, b=slope gene,m=memory gene

learning strategies in an environment with mixed and pure strategists. We were also able to answer some direct questions.

- When plasticity is prevented from evolving, almost all populations played mixed tactics with varying ratios of producing and scrounging, the rare pure tactic was seen in the population in certain conditions, but it would always die out.
- If plasticity is allowed to evolve, plastic strategies greatly outnumber non plastic strategies.
- In an environment where plasticity is allowed to evolve, plastic learning and non-learning strategies would have curved BRNs with positive slopes and a negative elevation on average. This suggests that these strategies tend to prefer scrounging in the absence of information, but as they gain information on their environment are more likely to produce. This is not the only option, variation seen in the fainter lines in Fig. 13 shows that individuals with negative slopes and positive elevations can appear.
- In environments where plasticity was allowed to evolve, plastic learning strategies outnumbered plastic non-learning strategies and non-plastic strategies. There would need to be a larger cost to memory than one used for non learning strategies to be more successful than learning strategies.
- In situations where plasticity is allowed to evolve and when it is prevented, how an environment changes and how fast it changes appears to be the root cause of variation in individual reaction norms. Faster speeds and variation between generations appear to reduce variation in these reaction norms.

7.1 Future Work

There are still areas of this model that can and should be explored further. First, no alternate environmental speed was run for the plastic scenario. This does leave a hole in our understanding of how environmental speed affects the evolution of plastic strategies. It would be interesting to see if subjecting the plastic scenarios to slow and fast environments would result in the patterns similar to those seen in the non-plastic scenarios or if strategy type preferences would be altered in any way.

This model has the capability to simulate different speeds and levels of environmental fluctuation within generations than between generations. Future work with this model could explore the effect of environments whose within generation fluctuation is not the same as the fluctuation found between generations. How would a population evolve in an environment that has smaller, faster fluctuations within generations, but very large, slow fluctuations between generations?

Another angle that could be approached is the addition of a reproductive cost. There must be a number of individuals whom are only just making the cutoff for surviving, but it is quite another hurdle to have the energy to both survive and reproduce. Adding a reproductive cost should cull strategies that are only able to support an individual, but not successful enough to grant it the energy reserves to be able to invest in reproduction.

There is a question if certain information types are more beneficial in specific environmental conditions or for specific strategies. As of this study they appear to be evenly split, but they were not fully investigated. Another item of interest that was not fully looked at was the presence of a pattern of fluctuating pattern of levels of adaptive and mal-adaptive strategies. Figures detailing the patterns of adaptive and mal-adaptive strategies can be found in the appendix attached.

Finally, in previous work this model utilized a "noise" gene to reflect within-individual and within-genotype noise. This current iteration of the model set this as a constant so that this would not have an affect on our results, but re-implementing this noise gene could have an effect on what kinds of strategies evolve.

Bibliography

Afshar, Mohammad, and Luc-Alain Giraldeau. “A unified modelling approach for producer–scrounger games in complex ecological conditions”. *Animal Behaviour*, vol. 96, 1 Oct. 2014, pp. 167–76. DOI: `10.1016/j.anbehav.2014.07.022`. (Cit. on p. 19).

Barnard, C. J., and R. M. Sibly. “Producers and scroungers: A general model and its application to captive flocks of house sparrows”. *Animal Behaviour*, vol. 29, no. 2, 1 May 1981, pp. 543–50. DOI: `10.1016/S0003-3472(81)80117-0`. (Cit. on p. 5).

Barta, Zoltán, and Luc-Alain Giraldeau. “Daily Patterns of Optimal Producer and Scrounger Use under Predation Hazard: A State-Dependent Dynamic Game Analysis”. *The American Naturalist*, vol. 155, no. 4, Apr. 2000, Publisher: The University of Chicago Press, pp. 570–82. DOI: `10.1086/303342`. (Cit. on p. 5).

Beauchamp, Guy. “A spatial model of producing and scrounging”. *Animal Behaviour*, vol. 76, no. 6, 1 Dec. 2008, pp. 1935–42. DOI: `10.1016/j.anbehav.2008.08.017`. (Cit. on pp. 5 / 6).

Bednekoff, Peter A. “Mutualism among Safe, Selfish Sentinels: A Dynamic Game”. *The American Naturalist*, vol. 150, no. 3, Sept. 1997, Publisher: The University of Chicago Press, pp. 373–92. DOI: `10.1086/286070`. (Cit. on p. 3).

Bell, Alison M., et al. “The repeatability of behaviour: a meta-analysis”. *Animal Behaviour*, vol. 77, no. 4, 1 Apr. 2009, pp. 771–83. DOI: `10.1016/j.anbehav.2008.12.022`. (Cit. on p. 9).

Bharath, Dhanya. INDIVIDUAL VARIATION AND PLASTICITY IN TACTIC USE IN A PRODUCER-SCROUNGER GAME A Threshold Trait Model. 27 Mar. 2023. (Cit. on p. 23).

Caraco, T., et al. “Dominance and social foraging: a laboratory study”. *Animal Behaviour*, vol. 38, no. 1, 1 July 1989, pp. 41–58. DOI: `10.1016/S0003-3472(89)80064-8`. (Cit. on p. 5).

Caraco, Thomas, and Luc-Alain Giraldea. “Social foraging: Producing and scrounging in a stochastic environment”. *Journal of Theoretical Biology*, vol. 153, no. 4, 21 Dec. 1991, pp. 559–83. DOI: `10.1016/S0022-5193(05)80156-0`. (Cit. on pp. 5 / 6).

Caraco, Thomas, Steven Martindale, et al. “An empirical demonstration of risk-sensitive foraging preferences”. *Animal Behaviour*, vol. 28, no. 3, 1 Aug. 1980, pp. 820–30. DOI: `10.1016/S0003-3472(80)80142-4`. (Cit. on p. 6).

Charnov, Eric L. “Optimal foraging, the marginal value theorem”. *Theoretical Population Biology*, vol. 9, no. 2, 1 Apr. 1976, pp. 129–36. DOI: `10.1016/0040-5809(76)90040-X`. (Cit. on p. 2).

Clements, KEVIN C., and DAVID W. Stephens. “Testing models of non-kin cooperation: mutualism and the Prisoner’s Dilemma”. *Animal Behaviour*, vol. 50, no. 2, 1 Aug. 1995, pp. 527–35. DOI: `10.1006/anbe.1995.0267`. (Cit. on p. 2).

Coolen, Isabelle, and Luc-Alain Giraldeau. “Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata*”. *Animal Behaviour*, vol. 66, no. 4, 1 Oct. 2003, pp. 657–64. DOI: `10.1006/anbe.2003.2236`. (Cit. on p. 5).

Davies, N. B. (Nicholas B.), et al. *An introduction to behavioural ecology*. 4th, Wiley-Blackwell, 2012, `archive.org/details/introductiontobe0000davi_j0v9`. Accessed 21/3/2024, (cit. on p. 2).

Dingemanse, Niels J., et al. “Behavioural reaction norms: animal personality meets individual plasticity”. *Trends in Ecology & Evolution*, vol. 25, no. 2, 1 Feb. 2010, pp. 81–89. DOI: `10.1016/j.tree.2009.07.013`. (Cit. on pp. 4 / 7).

Dubois, Frédérique, Julie Morand-Ferron, et al. “Learning in a game context: strategy choice by some keeps learning from evolving in others”. *Proceedings. Biological Sciences*, vol. 277, no. 1700, 7 Dec. 2010, pp. 3609–16. DOI: `10.1098/rspb.2010.0857`. (Cit. on pp. 6 / 7 / 15).

Dubois, Frédérique, and Étienne Richard-Dionne. “Consequences of multiple simultaneous opportunities to exploit others’ efforts on free riding”. *Ecology and Evolution*, vol. 10, 16 Apr. 2020. DOI: `10.1002/ece3.6201`. (Cit. on p. 18).

Dugatkin, Lee, and Hudson Reeve. *Game Theory&Animal Behavior*. Oxford UP, 5 Feb. 1998, DOI: `10.1093/oso/9780195096927.001.0001`. (Cit. on p. 4).

Hansen, Thomas F., et al. “On Adaptive Accuracy and Precision in Natural Populations”. *The American Naturalist*, vol. 168, no. 2, 2006, Publisher: [The University of Chicago Press, The American Society of Naturalists], pp. 168–81. *JSTOR*, DOI: `10.1086/505768`. (Cit. on p. 9).

Harley, Calvin B. “Learning the evolutionarily stable strategy”. *Journal of Theoretical Biology*, vol. 89, no. 4, 21 Apr. 1981, pp. 611–33. DOI: `10.1016/0022-5193(81)90032-1`. (Cit. on p. 2).

Henriksen, Rie, et al. “Intra-Individual Behavioural Variability: A Trait under Genetic Control”. *International Journal of Molecular Sciences*, vol. 21, no. 21, 29 Oct. 2020, p. 8069. DOI: `10.3390/ijms21218069`. (Cit. on p. 12).

Houston, Alasdair I., and John M. McNamara. “Switching between resources and the ideal free distribution”. *Animal Behaviour*, vol. 35, no. 1, 1 Feb. 1987, pp. 301–02. DOI: `10.1016/S0003-3472(87)80241-5`. (Cit. on p. 6).

Hutton, J. M. “Incubation temperatures, sex ratios and sex determination in a population of Nile crocodiles (Crocodylus niloticus)”. *Journal of Zoology*, vol. 211, no. 1, 1987, _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1469-7998.1987.tb07458.x, pp. 143–55. DOI: `10.1111/j.1469-7998.1987.tb07458.x`. (Cit. on p. 10).

Kacsoh, Balint Z., et al. “Drosophila species learn dialects through communal living”. *PLOS Genetics*, vol. 14, no. 7, 19 July 2018, Publisher: Public Library of Science, e1007430. DOI: `10.1371/journal.pgen.1007430`. (Cit. on p. 2).

Katsnelson, Edith, Uzi Motro, Marcus Feldman, et al. “Evolution of learned strategy choice in a frequency-dependent game”. *Proceedings. Biological sciences / The Royal Society*, vol. 279, 21 Sept. 2011, pp. 1176–84. DOI: `10.1098/rspb.2011.1734`. (Cit. on pp. 3 / 6 / 7 / 15).

Katsnelson, Edith, Uzi Motro, Marcus W. Feldman, et al. “Early experience affects producer–scrounger foraging tendencies in the house sparrow”. *Animal Behaviour*, vol. 75, no. 4, 1 Apr. 2008, pp. 1465–72. DOI: `10.1016/j.anbehav.2007.09.020`. (Cit. on pp. 2 / 5).

Lendvai, ÁdÁm Z., et al. “The effect of energy reserves on social foraging: hungry sparrows scrounge more”. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, vol. 271, no. 1556, 7 Dec. 2004, Publisher: Royal Society, pp. 2467–72. DOI: `10.1098/rspb.2004.2887`. (Cit. on p. 5).

Maynard Smith, J. “The theory of games and the evolution of animal conflicts”. *Journal of Theoretical Biology*, vol. 47, no. 1, 1 Sept. 1974, pp. 209–21. DOI: `10.1016/0022-5193(74)90110-6`. (Cit. on pp. 3 / 23).

McNamara, John M., and Olof Leimar. *Game Theory in Biology: concepts and frontiers*. Oxford UP, 24 Sept. 2020, DOI: `10.1093/oso/9780198815778.001.0001`. (Cit. on pp. 2 / 3 / 18).

Modelling Animal Decisions Group: et al. “The evolution of decision rules in complex environments”. *Trends in Cognitive Sciences*, vol. 18, no. 3, Mar. 2014, pp. 153–61. DOI: `10.1016/j.tics.2013.12.012`. (Cit. on p. 4).

Ohtsuka, Yasunori, and Yukihiko Toquenaga. “The patch distributed producer–scrounger game”. *Journal of Theoretical Biology*, vol. 260, no. 2, 21 Sept. 2009, pp. 261–66. DOI: `10.1016/j.jtbi.2009.06.002`. (Cit. on p. 18).

Orzack, Steven Hecht, and Elliott Sober. “How (not) to test an optimality model”. *Trends in Ecology & Evolution*, vol. 9, no. 7, 1 July 1994, pp. 265–67. DOI: `10.1016/0169-5347(94)90296-8`. (Cit. on p. 9).

Parker, Geoff, and J.M. Smith. “Optimality in evolutionary biology”. *Nature*, vol. 348, 1 Nov. 1990, pp. 27–33. DOI: `10.1038/348027a0`. (Cit. on p. 2).

Reid, Jane M., and Paul Acker. “Properties of phenotypic plasticity in discrete threshold traits”. *Evolution*, vol. 76, no. 2, 1 Feb. 2022, pp. 190–206. DOI: `10.1111/evo.14408`. (Cit. on pp. 4 / 19).

Roff, Derek A., et al. “THE EVOLUTION OF THRESHOLD TRAITS: A QUANTITATIVE GENETIC ANALYSIS OF THE PHYSIOLOGICAL AND LIFE-HISTORY CORRELATES OF WING DIMORPHISM IN THE SAND CRICKET”. *Evolution*, vol. 51, no. 6, 1 Dec. 1997, pp. 1910–19. DOI: 10.1111/j.1558-5646.1997.tb05113.x. (Cit. on p. 4).

Smith, John Maynard. *Evolution and the Theory of Games*. Google-Books-ID: Nag2IhmPS3gC, Cambridge UP, 21 Oct. 1982. (Cit. on pp. 3 / 4).

Templeton, Jennifer, and Luc-Alain Giraldeau. “Patch assessment in foraging flocks of European starlings: Evidence for the use of public information”. *Behavioral Ecology*, vol. 6, 1 Mar. 1995. DOI: 10.1093/beheco/6.1.65. (Cit. on p. 2).

Tóth, Zoltán, et al. “Effects of relatedness on social-foraging tactic use in house sparrows”. *Animal Behaviour*, vol. 77, no. 2, 1 Feb. 2009, pp. 337–42. DOI: 10.1016/j.anbehav.2008.10.005. (Cit. on pp. 5 / 18).

Turney, Shaun, and Jean-Guy J. Godin. “To forage or hide? Threat-sensitive foraging behaviour in wild, non-reproductive passerine birds”. *Current Zoology*, vol. 60, no. 6, 1 Dec. 2014, pp. 719–28. DOI: 10.1093/czoolo/60.6.719. (Cit. on p. 10).

Valone, Thomas J. “Group Foraging, Public Information, and Patch Estimation”. *Oikos*, vol. 56, no. 3, 1989, Publisher: [Nordic Society Oikos, Wiley], pp. 357–63. *JSTOR*, DOI: 10.2307/3565621. (Cit. on p. 7).

Vickery, William L., et al. “Producers, Scroungers, and Group Foraging”. *The American Naturalist*, vol. 137, no. 6, June 1991, pp. 847–63. DOI: 10.1086/285197. (Cit. on pp. 5 / 17).

Westneat, David F., et al. “The biology hidden inside residual within-individual phenotypic variation”. *Biological Reviews*, vol. 90, no. 3, 2015, _eprint: https://onlinelibrary.wiley.com/doi/pdf/10. pp. 729–43. DOI: 10.1111/brv.12131. (Cit. on pp. 9 / 12).

Westneat, David. F., et al. “Causes and Consequences of Phenotypic Plasticity in Complex Environments”. *Trends in Ecology & Evolution*, vol. 34, no. 6, 1 June 2019, pp. 555–68. DOI: 10.1016/j.tree.2019.02.010. (Cit. on p. 9).

Young, R. J., et al. “Risk-sensitive foraging in bitterlings, *Rhodeus sericus*: effects of food requirement and breeding site quality”. *Animal Behaviour*, vol. 40, no. 2, 1 Aug. 1990, pp. 288–97. DOI: 10.1016/S0003-3472(05)80923-6. (Cit. on p. 6).

NTNU

Norwegian University of
Science and Technology