Identifying the Evolutionary Conditions for the Emergence of Alternative Reproductive Tactics in Simulated Robot Colonies

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Degree Conferral Date	2020-06-30
Degree	Doctor of Philosophy
Degree Referral Number	38005甲第57号
Copyright Information	(C) 2020 The Author.
URL	http://doi.org/10.15102/1394.00001447

OKINAWA INSTITUTE OF SCIENCE AND TECHNOLOGY
GRADUATE UNIVERSITY

Thesis submitted for the degree

Doctor of Philosophy

Identifying the Evolutionary Conditions for the Emergence of Alternative Reproductive Tactics in Simulated Robot Colonies

by

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June,2020

Declaration of Original and Sole Authorship

I, FARZANA RAHMAN, declare that this thesis entitled “Identifying the Evolutionary Conditions for the Emergence of Alternative Reproductive Tactics in Simulated Robot Colonies.” and the data presented in it are original and my own work.

I confirm that:

- This work was done solely while a candidate for the research degree at the Okinawa Institute of Science and Technology Graduate University, Japan.
- No part of this work has previously been submitted for a degree at this or any other university.
- References to the work of others have been clearly attributed. Quotations from the work of others have been clearly indicated and attributed to them.
- In cases where others have contributed to part of this work, such contribution has been clearly acknowledged and distinguished from my own work.
- None of this work has been previously published elsewhere, with the exception of the following:
  Farzana Rahman, Kenji Doya and Alexander Mikheyev, ‘Identifying the Evolutionary Conditions for the Emergence of Alternative Reproductive Tactics in Simulated Robot Colonies.’, Artificial Life and Robotics conference (2020).

Signature: FRahman

Date: 22 June,2020

Abstract

Alternative reproductive tactics (ARTs), phenomena in which individuals within one sex adopt different tactics for accessing mates or raising offspring, are commonly observed in all major taxa. In order to study the ecological conditions for the emergence of ARTs, we developed an embodied evolution framework incorporating ecological features, such as body size and energy maintenance, where male and female robotic agents naturally face both intersexual and intrasexual interactions for survival and reproduction. Each agent has a decision neural network with extrinsic and intrinsic sensory inputs to choose one of four basic behaviors: mating, foraging, approaching and waiting. The reproductive success depends on the body size and the energy level of both male and female upon mating and it is assumed that only female carries the reproduction cost, as in nature the cost of male's sperm production is negligible relative to that of female's eggs. We performed simulation experiments in environments with different conditions (food density, reproductive cost, and male-female ratio) and found ARTs emerged both in males and females. Males evolved three kinds of alternative tactics - fixed genetically distinct ARTs (dominant and sneaker males that differ in body size and the tactic for getting access to female), conditionally flexible ARTs (individuals change tactics according to body size), and mixed ARTs (combination of genetically fixed and conditionally flexible ARTs). Females evolved to have two genetically distinct ARTs (quality oriented female, QoF, and number oriented female, NoF), where they increase fitness either by offspring quality or quantity. Analysis of the results confirms the experimental notions that male genetically fixed ARTs are strongly affected by intensity of sexual selection, male conditionally flexible ARTs are significantly affected by competition level, and female ARTs are mainly affected by food density. Analysis of ESS shows male ARTs are evolutionary stable with negative frequency dependent selection and female ARTs are evolutionary stable with both frequency and density dependent selection. To our knowledge, this study is the first to show the emergence of ARTs in both male and female from initially continuous characteristics in a simulated embodied evolution framework. The evolved ARTs are quite similar to the ARTs found in nature and provide insights about how interactions between the sexes are affected by and affect the evolution of ARTs within each sex. This framework is flexible enough to further analyze species of different sexual mechanisms (hermaphrodite, androdioecious, gynodioecious, etc.) and can be used as an important tool to understand the ecology of social interaction.

Acknowledgement

A PhD is a journey, which teaches us a new way of life. I would like to thank the peoples from my heart who helped me and was beside me to accomplish this journey.

My Supervisor, Prof. Kenji Doya, for years of his wise supervision, extreme patience and tremendous support. Building a thesis project in multidisciplinary field is quite challenging and sometimes risky. But when I wished to do such project, Prof. Doya never discouraged me. He supported me in all aspects and even in the time of my extreme family problem. Although I got depressed with the project sometimes, Prof. Doya never told me any negative or depressing word. He was always hopeful about this project and encouraged me to continue it. There is no word to thank him enough, for his extraordinary support through this journey.

My Co-Supervisor, Prof. Mikheyev, for his valuable advice and support on the biological aspects of the project.

My Academic Mentor, Professor Gordon, for supporting me all this way.

Dr. Eji Uchibe and Dr. Stefan Elfwing, the former member of the Unit, who provided invaluable support to understand and formalize a multidisciplinary project.

My Family, especially my husband, Md Mostafizur Rahman and my parents, for their mental support and prayers, which kept me going till the end of this journey.

Professor Gail Tripp, for being such a nice advisor and supporter in all kind of official and unofficial problem. She taught me the way of communication and also sometimes the meaning of life. Meeting her at OIST is my life long achievement.

Professor Jeff Wikens, the previous dean of the graduate school, who always supported students in their very crucial time. Talking with Jeff always gave me hope for continuing this journey.

Dr. Laura Sanger, my former psychiatrist at GANJU. Laura opened a new window of life for me. She made me understand the need of psychological support during depression. Discussing any problem with her was always enjoyable.

My friends at OIST, Lena, Sandrine, Shoko, Maria who always supported me in all aspects. I have such nice memories with all of them and some of the best memories of my life. Last few years of my PhD would be impossible without your mental support.

The Kaiholo Cafe owners, Mi san and Pi san, for making such nice pancakes and helping me to relax in my difficult time.

And Finally, the graduate school staffs who always supported with their best.

DEDICATION

I dedicate all my work to my mother Doctor Asma Khatun, who died during my PhD journey. She had sacrificed her all achievements to see me successful and happy. Even during her last days, she encouraged me to continue my PhD rather than returning home to take care of her. She couldn’t meet her beloved daughter at her deathbed. But whatever this daughter will achieve, will always be dedicated to her.

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Chapter 1

Introduction

Alternative Reproductive Tactics (ARTs), meaning individuals of one sex having consistent variation in reproductive behavior, such as territorial-parasitic, paternal-sneaker, satellite-calling, is observed in all major taxa including mammals, amphibians, insects and particularly in fishes [1]. Animals may evolve genetically discrete alternative reproductive tactics (ART) or, they may change tactics according to physical and environmental conditions [1,2]. ARTs are observed and investigated both in male and female, although male ARTs are more common. Male ARTs are often seen as investor and exploiter tactics [2,3], and female ARTs are often distinguished according to their mating frequency and investment in eggs [24]. Studying this consistent variation of reproductive tactics in male or female provides the opportunity to investigate the emergence and maintenance of phenotypic variation [1,2], which is one of the fundamental questions in evolutionary biology.

Researcher developed different biological [3,4] and mathematical [60,61] models to study the emergence of ARTs. Existing theoretical frameworks of Alternative reproductive tactics (mainly modeled by abstract mathematical models [60] or individual based simulation [42]) usually assume that there already exist two or three distinct phenotypes (with different tactic) and make prediction about the expected frequencies of different tactics in different situation. Also in these models agents have low embodiment with environment and important aspects of real life features between agents, such as occupied body space of the agents, sensory information about the environment, physical interaction with other agents, are not take into account. By contrast, how distinct types emerge from initially continuous variation of characteristics through evolution is a conceptually different question, which has been ignored by theoretical studies of ARTs, as they usually focus on how already present variations of reproductive behavior are maintained.

In this study, I develop an embodied evolution framework incorporating biological features (vision, physical interaction, energy maintenance, growth, mortality, reproductive cost, etc.) where male and female agents naturally face both intrasexual and intersexual interactions for survival and reproduction. Each agent has a decision neural network with intrinsic and extrinsic sensory inputs to choose one of four basic behaviors: foraging, mating, approaching, and waiting. As larger males have larger testes [48], which leads to higher reproductive success than smaller males [49], and larger females have higher fertility and fecundity [45,46], the reproductive success is assumed to depend on the body size and the energy level of both male and female upon mating. Females are assumed to bear the main cost for producing offspring, from her current energy level, as investing for sperms is negligible than the energy investment of eggs [31] and in most animals females have to bear and provide nutrition to the egg or offspring until they give birth or lay eggs [45]. I use this model to investigate whether and what types of male and female ARTs evolve from initially homogeneous populations.

Structure of the thesis:

The remainder of the thesis is structured in the following way-

In Chapter 2, the theory and the related approaches to understand the underlying dynamics of ARTs are reviewed, with an introduction to the research that inspired the development of the embodied evolution model of ARTs.

In Chapter 3, the proposed embodied evolution model is explained along with the parameters and assumptions, which introduces both natural selection and sexual selection in the model.

Chapter 4, 5 and 6 are the main result chapters. Chapter 4 explains the evolved male and female ARTs emerged in 450 populations with their evolved behavior. Chapter 5 provides the analysis of the male and female ARTs evolved in different environmental conditions (food density, reproductive cost, male density/competition level) and explains the effect of the conditions on the emergence of ATRs. In chapter 6, we did additional experiments to test the evolutionary stability (ESS) of male and female. Along with the ESS of male and female ARTs, the difference of evolved male and female ESS are also discussed.

Chapter 7 provides an overreaching discussion on the embodied evolution model and the results discussed in chapter 4,5 and 6, along with limitations and future direction. The whole work is wrapped up with key points with a conclusion and summery in chapter 8.

Chapter 2

Fundamentals and Related Work

This chapter introduces the fundamentals of the alternative reproductive tactics (ARTs), related works, existing models and discuss literature, which supports the assumption and inspiration for studying alternative reproductive tactics (ARTs) in embodied evolution framework.

2.1 Alternative Reproductive Tactics (ARTs)

Animals show peculiar and wonderful behaviors to meet their demand for surviving and reproduction. Individuals often compete with each other for limited foods and mates, to cope with direct and indirect costs and benefits of mating, which result in complex and interesting reproductive behaviors [1]. These reproductive behaviors, such as territorial protection, sneaking, displaying or other various approaches to obtaining a mate, are called 'Tactics' and the genetically based decision rules to maintain these Tactics is referred as 'Strategy' [16]. Alternative reproductive tactics (ARTs) evolve when individuals of same sex respond in two or more different ways to increase their reproductive fitness, which may occur in the forms of alternative body phenotypes and mating behaviors [2,3]. It is common across all major taxa, including, mammals (e.g. meerkat, *Suricata suricatta*; [5]), amphibians (e.g strawberry poison frog, *Oophaga pumilio*; [6]), insects (e.g. dung beetles, *Onthophagus acuminatus*; [7]), and particularly very common in fishes (e.g. bluegill sunfish, *Lepomis macrochirus*; [8] [9]). In dioecious systems (systems that contains two kind of sexually different individuals such as male and female), mainly two types of male reproductive tactics are seen (**Table 2.1**). One is the investor tactic where individual investing (e.g. defense, courtship, nest building, calling etc.) more on competition to get access to female. And the second one is the exploiter tactic (sneaking, non-calling, intercepting, etc.) where individuals exploit the investment of the investor tactic [4].

Table 2.1 Example of ARTs in animals

Species	**Investor tactic**	**Exploiter tactic**
Amphibians Example: strawberry poison frog [6]	Calling: Call for female and had larger body size to court female.	Non-calling/intercepting: small in size and intercepts females who comes to mate with calling males.
Mammals Example: waterbuck and kob [4]	Bourgeois/Territorial: Larger size and defends against other males to access female in it's territory.	Satellite/Sneaker: Smaller size and sneak to access female who comes to mate with larger male's territory.
Insects Example: Dung beetles [7]	Guarder/fighter: Larger in size and has weapon (such as horn) to guard female and fight with other males who tries to access female.	Satellite/Sneaker: Smaller in size, has no weapon and encounter female by sneaking guarder male's territory.
Fish Example: bluegill sunfish [8]	Parental/nest builder: Larger in size and build nest to attract female for fertilization.	Sneaker: Sneak fertilization of large parental males.

Females produce relatively few, highly nutritious gametes, whereas males produce more abundant, smaller, motile gametes. Because only a single gamete of each type is required to produce an offspring, there will be an excess of male gametes that will not fertilize any eggs. Therefore, males have to compete to access female and the alternative reproductive tactics are more common in males [3]. But females can have direct and indirect cost and benefit of mating and can also compete if access to high quality mates is limited. Female ARTs arise, for example, with differences in quantity of mates [20,21], as a result of mate conflict and coercion [22,23], differences in their investment for eggs or fecundity [24,25,26]. However, the key factors of mating strategy in female are their choice for offspring quality and the number of mates [27,110].

When multiple reproductive tactics emerge in a population, and individuals decide to apply one tactic throughout their lifetime, it is referred as ‘fixed ART’ [3,4]. For example, Woodhouse’s toads (*Bufo woodhousii*) males have satellite and calling tactic, where large adult males always apply the calling tactic and small adult male always apply the satellite tactic [17]. But if individuals switch between tactics according to certain conditions or thresholds, then it is referred as ‘flexible or conditional ART’ [3,4]. For example, male rubyspot damselflies (*Hetaerina americana*) have territorial and non-territorial tactics, where they switch between tactics according to their physiological difference in energetic quality [18]. Interestingly, males of some species can execute more than two different ART, where ‘fixed’ and ‘flexible’ ART can coexist. For example, in cicilid *Lamprologus callipterus*, three tactics co-occur: ‘fixed’ parasitic tactic, ‘fixed’ bourgeois tactic, and a conditional or flexible tactic where male switch between parasitic and bourgeois tactics [19]. The stable coexistence of alternative reproductive tactic is maintained by frequency dependent, condition dependent, status dependent or density dependent selection, where the average fitness of different tactics converges to an equilibrium, that is evolutionarily stable, at a certain frequency (for genetically polymorphic alternative behaviors) or some switch point (for condition or status dependent behaviors) [2,3,16].

2.2 Alternative Reproductive Tactics and Interaction Between Sexes

In general, Male and female mating behavior pattern is shaped by natural selection and sexual selection [28]. Natural selection operates on individual survival and fecundity, where sexual selection is a complex interplay between and within sex, which provokes differential mating success [29]. Sexual conflict between sexes arises when fitness of one sex reduced by the behavior of opposite sex and conflict between sexes can increase with the intensity of sexual selection [30]. As a result, male and female fitness and their pattern of evolved reproductive behavior affected simultaneously by interactions within sexes and between the sexes. For example, males produce small gametes with very little energy and female produce finite number of gametes each of which requires high energy [31]. As a result, male compete to get more access to females or their eggs [32] and females become choosy in mate selection to get the highest benefit by mating with the best quality male [33]. The intensity of female choosiness affects the successful mating probability and degree of competition in males. Also, female choosiness will create a conflict between sexes, as female will try to avoid mating with low quality males. In consequence, female mate choice and mating strategy will simultaneously affect the benefits and costs of male competition and thus male mating strategies. In the same time, the outcome of completion among males or the mating strategy determines the costs and benefits of female mate choice and re-mating frequency, thus the mating strategy of females [23]. Therefore, male and female ARTs should vary significantly with different intensity of sexual selection and sexual conflict. This concept is nicely pictured by Alanzo [23] in the **Figure 2.1** below-

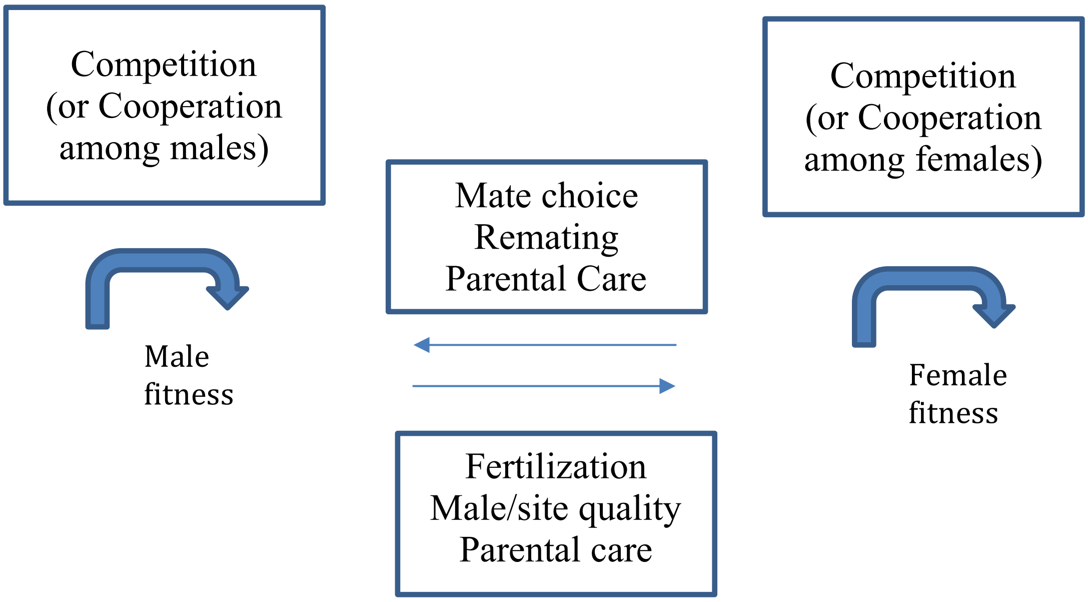

Figure 2.1 Interaction between sexes affects the reproductive behavior of each sex.

2.3 Models of Alternative Reproductive Tactics (ARTs)

Mitri et. all [43] classified the modeling approaches for understanding social behavior over a scale of 'situatedness', which they define as "the extent to which individuals are embedded in an environment that can be sensed and modified by those individuals". They explained it as situatedness spectrum by **Figure 2.2** [43], where abstract mathematical model has the lowest situatedness and living organism has the highest situatedness. Observing evolution in living organism is very rarely possible. Although we can do fieldwork and laboratory experiment with living organism, manipulating the behavior of each individual to analyze the response of remaining group members is almost impossible. Also, we can't test parameters for thousands of generations in a systematic way. We can't infer how different evolutionary parameters exactly interact and manipulate observed behavior, because we can't access and infer individual's decision making process through evolutionary generations. Therefore, although we can have broad outline of the evolution of the alternative reproductive tactics from field and laboratory experiments with living organism, to predict complex interactions between individual physiological conditions, prevailing environmental conditions, time constraints, and factors leading to frequency or density dependent selection within a population, researchers worked with different modeling approaches. In this part, I will review modeling approaches to study alternative reproductive tactics according to situatedness (**Figure 2.2**) and what new approaches now we should focus on to reveal more novel aspects of ARTs.

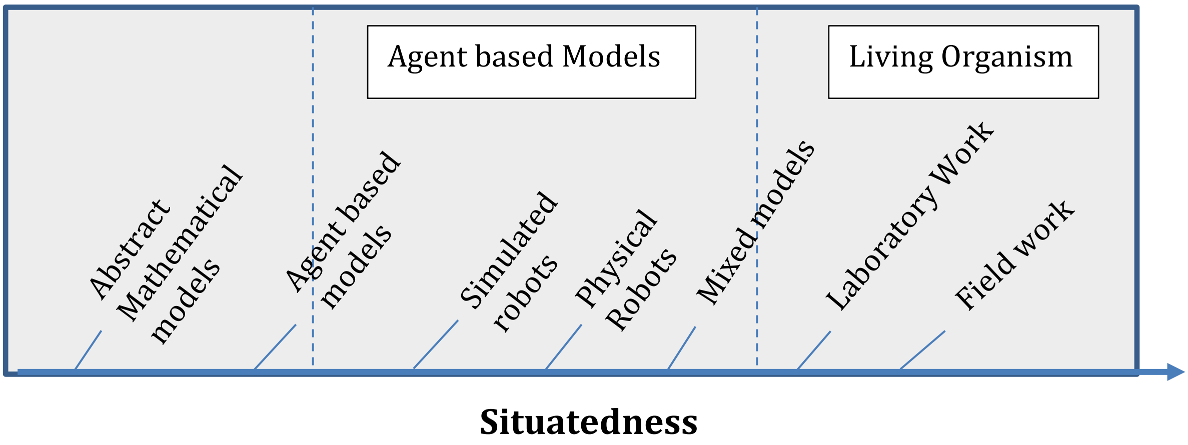

Figure 2.2 Social behavior study approaches on the scale of situatedness [43].

2.3.1 Abstract Mathematical Models

Researchers tried to understand the aspects of alternative reproductive tactics using different mathematical models such as dynamic games and game theoretic approaches. Most of them focus on male mating tactics. Earlier in 1995, Lucas et al. [60] took a dynamic game approach to evaluate how three male alternative mating tactics: satellite, call, or leave, differ in their mating success in density and frequency dependent conditions with six major predictions. Later with flexible caller/satellite dynamic game model, they showed that female arrival rate is a very important factor to shape the mating tactics in different conditions [61]. Skubic et al. [62] focused on the male parasitic tactic in a dynamic game model of cooperative breeder and explored the parameters under which a helper male parasitizes reproduction. From the model they found that “expulsion risk” might be the most important factor to regulate the parasitic behavior.

Although researchers started with modeling mostly male tactics, soon interaction between sexes came into focus. Henson and Warner first proposed a new approach [63] in fish alternative reproductive tactics with intersexual dynamics. They discovered that female alternative reproductive tactics exist and interaction between male and female can influence each other. They described the importance of considering female behavior and building a new model including intersexual interaction to get precise understanding about male and female reproductive tactics. Focusing on this intersexual interaction, Alonzo and Warner [65] studied a dynamic game model and field experiment data of Mediterranean wrasse mating behavior. They found that there is a sexual conflict with females and sneaker males, where female interaction and conflict with sneaker males play important roles. They also built a multiplayer dynamic game model to formalize how female choice can influence male alternative reproductive tactic. They discussed about six biological scenarios, each containing two types of male mating tactics, where males interact with each other in a frequency dependent or condition dependent manner. They concluded that female choice could significantly change male reproductive tactics in different situations [64]. Later Alonzo took a game theoretic approach [66] and predicted that interaction between the sexes can alter prediction of mating theory. Rather than any specific species and phenotypic difference in male or female population, she modeled male and female fitness affected by the abundance of resource in a site and concluded that without simultaneously considering the effect of resource and interaction within and between sexes on fitness, one can come to false conclusion about the pattern of selection among sites.

Female alternative tactics also gained importance, but far later than male ART studies. Luttbarg [67] modeled female mate assessment behavior by a dynamic game model. He tried to formalize female’s accurate or inaccurate assessment and different assessment cost to predict male quality and showed that female choice and assessment behavior could significantly shape male alternative behavior in different situations. More recently, Brenan et al. [68] used a game theoretic model and assessed female mate choice alternatives. They explicitly consider two reproductive tactics of females: direct assessment of male quality and copying the choice of other females. They postulated that female alternative behavior may get affected by male quality and female assessment error and tested female reproductive tactics in different situations.

Although these abstract mathematical models can provide powerful predictions, they have some major limitations. For example, usually they model the populations as a whole, and also neglect or strongly simplify local interactions among individual agents, their spatial environment, their phenotypic plasticity, and life-cycle dynamics. [43].

2.3.2 Agent based Models

To deal with the above limitations of abstract mathematical models, researchers developed agent-based models [69], which are also called individual-based models (IBMs), where ‘agents’ are modeled individually to understand social behaviors. Agent based models allow one to consider individual properties such as age or size along with their possible interaction with each other. ART researchers also lead to develop agent based model to include these individual based properties and make more realistic prediction about reproductive tactic.

Earlier Rowell et al. generate an Individual based simulation model of field cricket having calling (invest energy to call female) and satellite (sneaking female who comes to mate with calling male) alternative reproductive tactic. With the model they suggest that population density and sex ratio changes during the breeding season are important factors determining mating success of calling and satellite males [70]. Walker and Cade [71] modified this model to explore calling and satellite male fitness when parasitoid flies are present in the environment and found that risk of parasitism strongly influences the coexistence of alternative reproductive tactic. Recently, influenced by these previous studies, John et al. [72] modeled caller and satellite field cricket behavior in Individual based simulation with varied population density, sex ratio and female behavior and showed how parasitoid pressure can shape satellite and calling behavior in males.

Along with male reproductive tactics, recently researchers started to model female reproductive tactic with agent based model. Bleu et al. [27] studied female’s reproductive tactic according to mating cost, population density, and sex ratio. They used an individual based simulation where female had to choose male according to their acceptance threshold, which they evolved in generations. Females have to face the tradeoff: if they choose high acceptance threshold for males, then there is a high chance to be unmated. Instead; if they choose low threshold, then they can mate more but have to mate low quality males and take more mating cost. Their study shows most of the females in the population converge to a threshold and having high or low threshold than the common threshold is not beneficial. Also, they checked how female’s common acceptance threshold sensitively changes with population density, sex ratio, and mating cost.

Most recently, Engqvist and Taborsky [42] studied male alternative reproductive tactic in individual based simulation in a novel aspect. Rather than assuming distinct phenotypic variation in the model, they aim to predict the ecological and social conditions to evolve ART in males. For that, they modeled a territorial competition scenario with indeterminate growth, where growth rate and size dependent sperm investment were evolving variables. They tried to clarify the factors for the evolution of genetic and conditional reproductive tactics in the converged population. Their result showed that two or three fixed or conditional tactics could emerge in males according to their investment in growth and sperm. But in this agent based model, they did not include female interaction with male and the reproduction was asexual. As intersexual interaction is an important factor, to have complete scenario, it is necessary to build a model including female agents where male and female ARTs can evolve together.

In an actual system of living organism with highest 'situatedness' (Figure 2.2), each individual is fully embedded with environment, and make complex interaction with environment to take decision about their own behavior. Although agent based models considers individual property, it deprives important aspects of social behavior as individuals do not interact with environment with their perceptual and physiological information and have less embedded with environment.

2.3.3 Robotic agent Models

To bridge this gap, recently robot models are introduced as a new tool to study social behavior, and it has quickly gained importance in this research area. A robot is defined as a machine that can physically interact with it's environment and performs some sequence of behaviors, either autonomously or by remote control [73]. There are mainly two types of robot modeling approach, simulated robot and physical robot.

Simulated Robot model: The computer simulations of physical robots along with its interacting environment is defined as simulated robots, and become attractive tool for modeling because [43]-

a) As simulated robot model mimics physical robot along with its physical environment and considers perceptual, spatial, and resource related constraints. Therefore, it plays a role as the intermediate level on the situatedness scale (Fig. 2.2) between IBMs and physical robots' experiments.
b) Rather than conventional agent based model [42,27] simulated robots have three characteristics explained in [43]: " (i) they have an extended body (i.e. they occupy space in the world) rather than being a point; (ii) they gather information about the environment through sensors that are morphologically located and limited in range and accuracy rather than having an ideal perceptual system that can access global

and perfect information; and (iii) they move in an extended space with finite distances and resources rather than in mathematical spaces which often have no boundaries and/or infinite resources. All these factors can significantly affect the outcome of social behaviors that imply physical and perceptual interactions within a confined space.”

c) In terms of modeling social behavior, increasing model situatedness also reduces the risk of ignoring valuable properties of physical environment. For example, Mitri et al. [74] studied evolutionary emergence of communication in a group of simulated robots and found that, when foraging robots clusters around the food source, it becomes inadvertent information of food location for other robots

d) We can model robot brain or controller using neural network, where robot take perceptual information as input, decide own behavior, and interact with and adapt to the environment as an autonomous agent. Therefore, they can be used to build autonomous artificial organism model (described more in later part).

e) Using physics-based robotic simulations, numerous experiments can be performed with a large number of individuals in limited time frame, which is a significant advantage over using physical robots.

Physical Robot model: Along with the advantages of simulated robots (a-d), physical robot model includes the law of physics for free. Therefore,

a) It has highest ‘situatedness’ (Figure 2.2) and it became a very important tool for modeling social behavior when physical properties of the environment have significant effect on social interaction [43]. For example, Jeanson et al. [74] used IBM and Garnier et al. [75] used physical robot model to mimic the behavior of cockroaches. It was found that physical robot models match better with empirical data as Jeanson et al. [74] in IBM did not include the physical property of hiding behind each other in the simulated software agents.

b) Physical interaction between individuals in a robotic system can influence their movement relative to each other, which is very rarely taken into account in agent based models. Krieger, Billeter & Keller [93] demonstrated that the role of physical interaction between individuals is an important issue. They studied a group of small ant like robots programmed to collet scattered object and found that larger group has low foraging efficiency, as there was high interference in robots.

c) Moreover, physical robot model includes the effect of friction, body shape or robot morphology, which has been found very crucial for collective behavior [76].

Problems of using Physical robots:

Although Robot models are attractive over other agent based models, it is possible to face some difficult constraints. Setting up and experimenting with physical robots usually need quite longer time. They often need expensive hardware and if the robots break, it can take a long time and much cost to fix. Also, physical robots might not directly capture some aspects of living organism, such as changing weight according to food consumption or age, the physical change of the living organism in their development stage of life. To overcome these limitations, researcher prefers to use simulated robot model initially for their study.

2.3.3.1 Evolutionary Robotics (ER)

Evolutionary robotics is a framework where simulated or physical robots as autonomous artificial organism evolves their own behaviors by interacting with the environment [77]. It has become popular because of high situatedness in the environments [79,83,99]. The general concept of evolutionary robotics follows the famous theory of 'Natural selection' is very nicely explained by Floreano et al. [77] as follows. A population of distinct genomes is generated, where each of them contains the parameters defining the controller or morphology of a robot. Each genome contains stream of characters that can be translated as phenotype resembling different level of biological realism. When artificial neural network is used to determine robotic agents' behavior, the genome contains the synaptic connection weights of the neural network. The input of the neural network is the robot's sensory information and the output is the motor control of the robot. Each robotic agent has different genome having different synaptic weights for the network synaptic connection. Thus each robotic agent has different neural network in a population. Therefore, when each individual faces sensory-motor interaction with environment, they behave differently. The robot's fitness is then calculated from these behavioral differences such as how good the robot can avoid obstacle or how fast it can reach to a destination. At beginning, all robotic agents contain random values in their genes and show totally random behavior. According to Darwinian selection the genomes of the robots having highest fitness is then selected to generate next robot generation. To create new generation recombination and random mutation is applied on the selected genomes. Then this process is repeated over generations until stable behavioral scheme is achieved.

Both physical robots and simulated robots might be used to perform an evolutionary robotics experiment. Using simulated robots, physics based simulator allows to perform evolution in larger number of robots in limited time and later the resulted behaviors can be implemented in physical robots incorporating the evolved genome to test if the same behaviors are observed.

2.3.3.2 Embodied Evolution (EE)

Embodied evolution (EE) is a distributed and on-line version of ER, where a large number of robots interacts with each other in an environment and perform some task. Robots exchange their genetic information by mating (physically contacting with each other) and produce offspring for the next generation. The probability of producing offspring, i.e. their fitness, depends on their performance of the specified task in the environment. Therefore, the autonomous, asynchronous and distributed property of biological evolution is resembled by EE. This methodology of ER was introduced by Watson, Ficici, and Pollak [99,100]. Although the embodied evolution framework outperformed ER in some studies of surveillance and self-localization [101,102], it should be interesting in the study of evolutionary biology because of its more biologically plausible property. In the next section, I review the evolutionary biology studies using ER and EE models.

2.3.3.3 Robotic agent models (ER and EE) in evolutionary biology

To understand the general principle of evolutionary biology, scientists construct mathematical and simulation models. Although mathematical modeling and simulation provide deep insights into evolutionary questions, sometimes they meet their limit for simplification of different aspects, which is required to construct the model. To bridge this gap between real biological systems and models in explaining reasons for evolved behaviors is very challenging, because observing evolution in real time is extremely difficult and rarely possible. Although we can find a rare example of Weiser et al. [52] who did in-vitro bacterial evolution experiment for 25 years, their limit is clear, as it is not possible to experimentally observe the generations of slow evolution of species in real time. Therefore, it becomes a huge challenge to study evolution under realistic assumptions and realistic time frame [78]. To deal with this challenge, recently evolutionary robotics gained traction to model evolution with embodied agents that interacts with real environment. With highest situatedness, robot models act as artificial animals and it is possible to study from their interaction with environment, how particular behavior that we observe in nature has evolved by changing different parameter settings with high degree of freedom. Moreover, robot evolution has several advantages over biological studies, such as computing huge generations of robot controllers in a short time frame, easily replicating and repeating the experiment with multiple parameter settings in different environmental conditions. These features not only provide platforms for better quantitative testing, but also help in analyzing robustness and stability, when agents have complex realistic physical interaction with the environment and other agents.

Within the last decade, evolutionary robotics has been used to study a number of key issues in evolutionary biology [59]. Floreano and Keller with different co-authors [79-82] investigated different evolutionary phenomenon using robot evolution model. For example, the reliability and emergence of communication, Hamilton's rule for altruism [83], and social insect’s division of labor influenced by genetic architecture or mating frequency [84]. Evolution of cooperation and altruism was also studied by Montanier and Bredeche [85,86,103], Waibel et al. [87] and Solomon et al [88] using robot models. Robot evolution models are used to understand evolved morphological complexity [89,90], collective swarming behavior [91]. Most of these robot evolution studies were first done by simulated robots and then the result was investigated with physical robot for further understanding. Embodied Evolution models also gained traction in biologically motivated studies. One of the examples is the study of Long et al [104] who evolved swimming fish robot to investigate the evolution of vertebrates. They did their experiment with physical robot model in real time and provided an example that embodied evolution can be an important tool to investigate extinct and living species. Most recently, ‘Robot baby Project’ by Eiben et al [104] gained attention to researchers. They demonstrated real robot reproduction for the first time through embodied evolution. This ‘proof of concept’ study can work as a basis for developing future intelligent robots, which will evolve both functionally and morphologically.

Although robot evolution models are increasingly used to study evolving behaviors, in terms of investigating alternative reproductive behavior, it has been very limited. One related study was done by Da Rold et al. [92], who co-evolved a population of male and female robots in a simulated environment, where they eat food to live and reproduce by touching the opposite sex. The only difference between male and female robot was, the female robot is nonproductive for some time period. Also, the sexual dynamics was not incorporated into the evolutionary algorithm and their reproduced offspring were not generated by genetic exchange (crossover and mutation). Instead, males and females evolved separately, where the fitness function was based on the number of matings, although individual’s evolution depends on the interaction between the two types of robots. There they investigated variation in mating success and some behavioral difference between male and female if males do not have parental certainty. Although this study revealed some behavioral differences in male and female, there was no sexual reproduction and they did not find any discrete phenotypic variation in male or female.

Most recently, Elfwing et al. [59] investigated alternative reproductive tactics in a robot evolution model. He used embodied evolution technique, which is more biologically plausible as the robots reproduce offspring by mating, that is, a pairwise exchange of genotypes. The robots were hermaphrodites as they send and receive genotype with each other, that is play both male and female functions. In the study they found two types of genetically different phenotypes in their hermaphrodite robot population, who have different reproductive tactics named foragers and trackers. Trackers follow other agents for courtship by choosing mating module even when their energy level is low. Foragers mate only when they are fully charged, when the probability of successful reproduction is higher. In this study agents choose their behaviors according to their energy level and sensory information. Although this study was very simplified according to biological viewpoint (size, age, reproductive cost etc. were not included), this study gives light on the way in which alternative reproductive tactics can be studied with robotic model. If we can evolve alternative reproductive tactics in such a realistic artificial system, we can gain novel aspect of evolution from that.

2.4 Important properties in modeling the full picture of ARTs

In pervious sections, I reviewed the biological aspects and the models used to investigate the emergence of ARTs. From the investigation done in these studies, it become prominent that to explain the whole picture of ARTs in a model, three important properties should be included [2,3,16,98] –

1. Intersexual and intrasexual Interaction: Male and female evolve together in nature. Therefore, to understand how ARTs emerge, there should be male and female evolving together with intrasexual and intersexual interactions [23,2]. There should be the effects of both natural selection and sexual selection in the model.
2. Emergence from initially continuous characteristics: The existing theoretical studies [39,16] that attempted to model genetic architecture and coexistence [40,41] of ARTs assumed that two or three distinct phenotypes were already present in male or female. In contrast, to investigate the emergence of ARTs,

evolutionary emergence of distinct types in male and/or female, from initially continuous variation of characteristics should happen. That has not been addressed by the previous theoretical studies of ARTs, as they usually focused on the maintenance of already present variations [37,38,39].

3. High level of situatedness: Real animals in biological scenario have the highest situatedness. Therefore, to investigate the real picture of ARTs, we should make our model as highly situated as possible to capture more realistic feature, such as
    - Having a body shape, which actually occupies space according to its size rather than being a point.
    - Having local sensors with limited ranges, rather than perceptual view containing global information.
    - Moving in a space with finite dimensions and limited energy resources, rather than in mathematical spaces with arbitrary scaling.

    Each of these factors can significantly affect the interaction between agents as well as their behavior with each other.

2.5 Research Plan

In this chapter, I reviewed the fundamentals of ARTs and discussed the computational models relevant for studying ARTs. From the related literature, I pointed out the three important properties needed to investigate the full picture of ARTs. On this basis, I construct an original approach with the highest level of 'situatedness' (embodiment with environment like real organism) to model general situations where male and female agents satisfy basic constraints of life (finding food and mate) and interact in different reproductive condition, to produce alternative reproductive behavior from continuous characteristics in different environmental situation. For this purpose, I perform artificial evolution experiments with a colony of simulated robots using embodied evolution framework, where robots exchange genotypes physically to reproduce offspring and decide their behavior using their sensory and internal information while interacting with the environment. I apply this model to unravel and analyze under which ecological and social condition (competitive circumstances) two or more reproductive tactics spontaneously evolve, while agents face both intrasexual and intersexual interaction. The model does not make specific assumptions about whether reproductive tactics are frequency dependent (tactic's fitness depends on it's frequency in the population) or condition dependent (tactic's fitness depends on individual's conditions, such as size and age). Instead, these attributes will evolve and give conclusions about which behavioral choice is likely to emerge in which situation. In chapter 3, the embodied evolution model is explained with the description of underlying assumptions and parameters. The evolved male and female ARTs in different environmental condition are illustrated in chapter 4,5 and 6.

Chapter 3

Survival and Reproduction Model

In this chapter, I construct an embodied evolution model incorporating the three key properties identified in the previous chapter (section 2.4) for investigating the emergence of ARTs, namely, intersexual and intrasexual interactions, emergence from continuum, and situatedness.

3.1 Basic model Assumption

We consider a general situation where male and female robotic agents satisfy the fundamental constraints of life, namely survive and reproduction, and interact in different ecological condition to produce offspring. The simulation environment is designed for smart phone robots being developed by my colleagues at Neural Computation Unit (**Figure 3.1**) [95]. Each robotic agent has two wheels, a camera, accelerometer, and other sensors.

Figure 3.1 Smartphone Robots [95].

Male and Female robots use different body colors to distinguish each other. Each robot has a restricted visual area in the front and can measure the angle and distance to the nearest energy source, male and female agents. In this chapter, I explain the basic assumptions of the model and the design of the embodied evolution experiment.

3.1.1 Body Size and Growth

The body size is often highly correlated with reproductive success [44]. Large males can invest more for reproduction, such as building nest, winning territory or competition, giving protection to offspring from predators [4, 20,39], and can produce more sperm required for larger ejaculates, which has been found more advantageous when sperm competition occurs [48,49]. Females also benefit from larger body size, as they can produce high quality or high quantity of eggs or can invest high energy in reproduction [45,46]. Some species (birds, mammals, insect) have determinate growth that is they grow to a fixed size when they get mature, and some species (fish, reptile etc) have indeterminate growth, that is, they continue to grow throughout their life. As alternative reproductive tactics are more common in species with indeterminate growth, I adopt an indeterminate growth model. Usually the body growth rate is highest during early life stages, and reduces with increasing size and age [47]. To capture this, I use Van Bertalanffy growth equation [47], where the rate of change in size S is described as

$$\dot{S}(t) = K(L - S(t)) \quad \dots (i)$$

where
L: asymptotic body size when growth is zero.
K: growth rate.
$S(t)$: current body size.

Individual's growth depends on the stored energy level. Therefore, I take the agent's stored energy level $E(t)$ over some threshold E_0 as

$$E_{diff}(t) = \begin{cases} E(t) - E_0, & E(t) \geq E_0 \\ 0, & E(t) < E_0 \end{cases}$$

and assume that the growth rate K depends on E_{diff} as

$$K = \alpha E_{diff} \quad \dots (ii)$$

Thus the change of body size, $\dot{S}(t)$ is (from equation i & ii)-

$$\dot{S}(t) = \alpha\, E_{diff}(t)(L - S(t)) \ \ldots (iii)$$

Maternal phenotype significantly affects offspring quality [45,46]. Females with larger size can produce larger offspring and also female's health condition (nutrition and energy intake) affects offspring's nutrition during birth. Therefore, I assume that agent's initial size and energy depends on the maternal condition (size and energy) upon reproduction:

Initial size, S(0) = Maternal size ×0.2, or the minimal value S(0)=10

Initial Energy, E(0) = Maternal energy×0.2

3.1.2 Mortality

Mortality of an agent depends on both its energy level and body size. Agents gain 50 units energy by obtaining a food. When an agent's energy level becomes zero, it dies. Larger body size needs higher energy cost for maintenance. Also, several studies [106,107,108] demonstrate that high growth rate incurs high energy cost in addition to maintenance of the body. In our model, each time step, agent's energy cost incorporates costs for both growth and body maintenance as-

Energy cost, $EC(t) = \beta \times \left(current\ size\ S(t) + growth\ rate\ K(t)\right) \ldots (iv)$

Bigger individuals have low mortality rate and smaller individuals have higher mortality rate for different environmental reasons, such as predation [55-57]. Therefore the mortality of each agent is modeled as [58,95]-

$$M(S) = M_i + M_d e^{-(\frac{S}{S_0})} \ldots (v)$$

where,

$M(S)$: mortality with body size S.

M_i : size-independent mortality.

M_d: mortality change with body size

S_0 = the body size, at which size-dependent mortality drops to 1/e = 36.8% relative to that with the body size $S = 0$.

3.1.3 Intersexual Interaction

The intersexual interaction is modeled with a joint reproductive condition and the reproduction cost of male and female.

Reproductive condition: Reproductive condition is the probability of fertilization success and having offspring in next generation depending on the state of the male and female.

Larger males can invest more for mating (courting female, building nest etc) and have high competitive ability to get access to female [4]. Moreover, usually larger males have larger testes [48] and males with larger testes have been documented to have higher ejaculate rate to achieve higher reproductive success rates than males with smaller testes [49]. Male's health condition and energy level is also important for successful reproduction as at low energy and nutrition males tend to produce less sperm and invest less in reproduction [50]. Therefore, the reproductive condition for a male is designed as

$$\boldsymbol{R_M = R_{MS}\frac{S_M}{S_{Max}} + R_{ME}\frac{E_M}{E_{Max}}} \ldots (\boldsymbol{vi})$$

$Where, R_{MS} + R_{ME} = 1$

$E_M = Male\ current\ energy$
$E_{Max} = Maximum\ energy$
$S_M = Male\ current\ size$
$S_{Max} = Maximum\ size$

For females, health condition, which generally depends on the internal energy level, is a very important factor for successful reproduction, because most commonly they have to produce costly eggs [31] and bear the main reproduction cost (producing eggs or offspring). Size is also important for female reproductive success as large size females have high fertility and fecundity [45,46]. Moreover, females having large size have high probability of having offspring in next generation, as they can invest more on offspring such as protecting offspring from predators. Therefore, the reproductive condition for female is modeled including the effect of size and health condition-

$$\boldsymbol{R_F = R_{FS}\frac{S_F}{S_{Max}} + R_{FE}\,\frac{E_F}{E_{Max}}} \qquad \ldots(vii)$$

$$Where, R_{FS} + R_{FE} = 1$$

$E_F = Female\ current\ energy$
$E_{Max} = Maximum\ energy$
$S_F = Female\ current\ Size$
$S_{Max} = Maximum\ size$

When a male and a female mate, the probability of reproductive success of having offspring is dependent on the reproductive conditions for both male and female as

$$\boldsymbol{R_P = \frac{R_M + R_F}{2}}$$

$$\boldsymbol{= \frac{(R_{MS}\frac{S_M}{S_{Max}} + R_{ME}\frac{E_M}{E_{Max}}) + (R_{FS}\frac{S_F}{S_{Max}} + R_{FE}\,\frac{E_F}{E_{Max}}\ )}{2}} \quad \ldots(viii)$$

Reproductive cost: Males produce small gametes with very little energy and females produce limited numbers of gametes, each of which requires high energy. Investing for sperms is much cheaper and sometimes negligible than the energy investment of eggs [31]. Moreover, female have to bear and provide nutrition to the egg or offspring until it gives birth or lay eggs and offspring quality depends on maternal phenotype [45]. Therefore, we assume asymmetric reproductive cost in male and female. When male mates with female and if the reproductive condition is satisfied, the female have to bore the main cost **C_R** for producing offspring, from her current energy level. This asymmetric cost is very important for intersexual interaction. Because, when this cost is high, the number of matings during a female's lifetime is limited, which can increase the intensity of sexual selection and the conflict between sexes.

3.2 Robot Controller

The male and female robot controller consists of a two-layered control architecture, based on the framework in **Figure 3.1**, proposed by Stefan Elfwing et al. [94]. The top layer is a linear feed forward neural network which uses N_x dimensional input representing the environment and the agent's own state and decides to select from N_m behavioral modules according to $\text{argmax}(W\boldsymbol{x})$, where W is the neural network weight matrix (size of $N_m \times N_x$) and $\boldsymbol{x}$ is the current state input vector (size of $N_x \times 1$). The selected module controls the basic behaviors of the agents, namely, foraging, mating, approaching, and waiting. I consider that the agents already have learned to execute the basic behaviors and that evolution of the weights W affects how to select the appropriate basic behaviors under different situations [94].

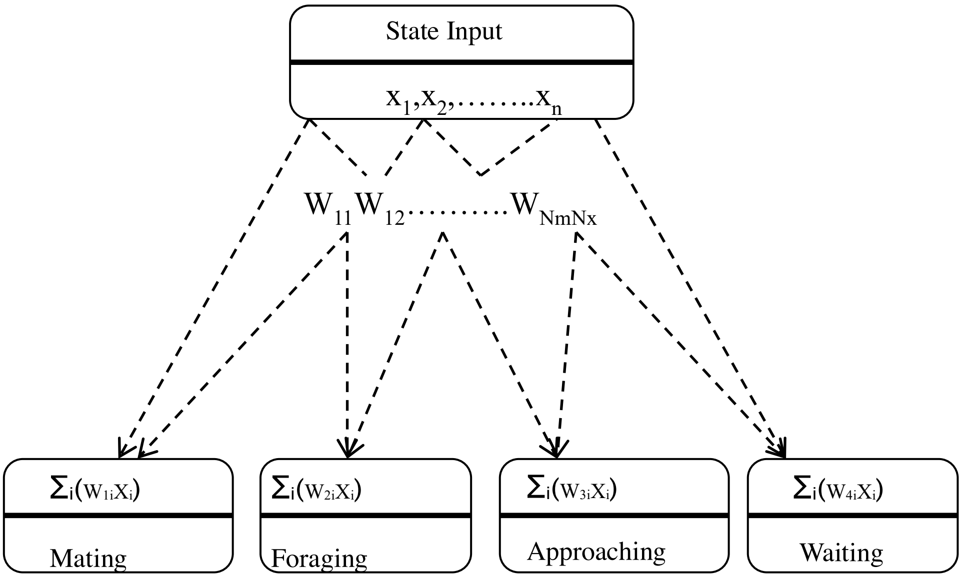

Figure 3.2: Basic Two-layer robot control architecture.

The behavioral modules and the top layer input of male and female robot controller is described below.

Behavioral modules: The robots can execute four basic hand-coded behaviors as follows.

Foraging: Find food (battery or energy source) in the environment. The agent takes the information of nearest food source, approaches to it, and consumes it to increase stored energy.

Mating: If a mating partner is visible within certain angle and distance, try to mate to produce offspring. The male robots can exchange genotype with only female robot and female robots can exchange genotypes only with male robots. Mating has three states: premating, mating, and postmating states. At first, an agent is in premating state. If it finds mate within a certain angle and distance, it can enter into the mating state. If the mating is successful with the probability defined by the reproductive condition ($viii$), the agent enters into postmating state and cannot choose mating module for some time period. Otherwise it returns to premating state. After the postmating time period, it enters into premating state and mate again or choose another behavior.

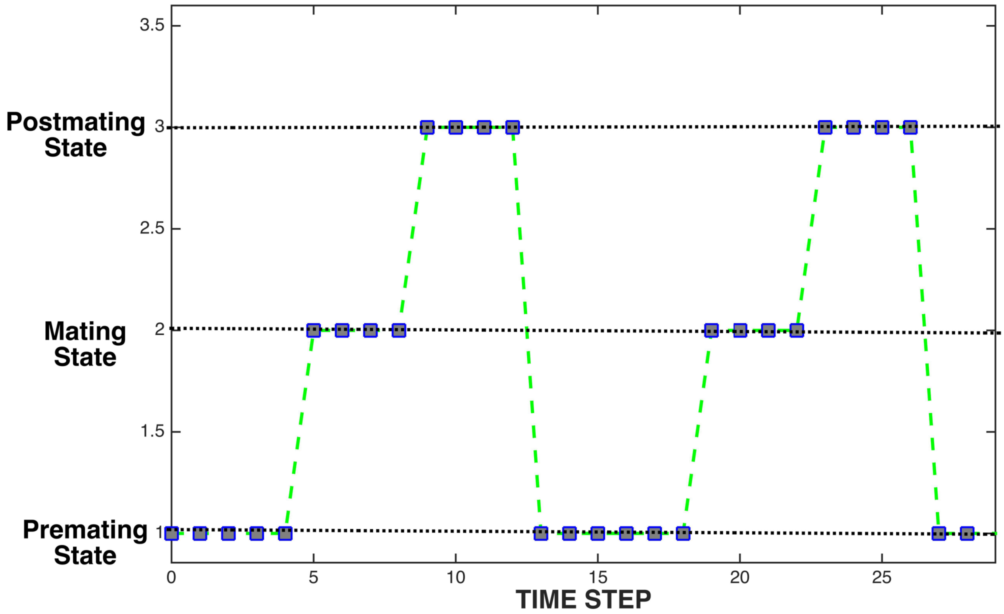

Figure 3.3 Changing of mating state of an agent acting mating module.

Approaching: approach toward the nearest agent and push it upon contact. With this module agents can interrupt each other in mating and food finding by pushing away from food or mate. The pushing ability depends on the size of the body.

Waiting: Stay at the current position. Waiting also cost energy depending on the agent's size.

Neural network controller: The input state of the top layer neural network for male and female robot is given bellow. The distance to the objects are normalized by the maximum range of vision.

x_1: *Constant bias of 1;*

x_2: *Gender: male=1, female=0 ;*

x_3: *Mate state: 1 if in premating state, otherwise 0;*

x_4: *Normalized energy level* $E(t)/E_{Max}$ *;*

x_5: *Normalized body size* $S(t)/ S_{Max}$ *;*

x_6: *Normalized age* t/t_{life}*;*

x_7: *Normalized size of the closest male,-1 if no male visible;*

x_8: *Normalized distance to the closest male face,-1 if no male face visible;*

x_9: *Normalized distance to the closest male back, -1 if no male back visible;*

x_{10}: *Normalized distance to the closest female face, -1 if no female face visible;*

x_{11}: *Normalized distance to the closest female back, -1 if no female back visible;*

x_{12}: *Normalized distance to the closest food, -1 if no food visible;*

The same inputs, such as x_7 to x_9 for the vision of a male, can be used differently by males for intrasexual competition and by females for the choice of mating partner.

3.3 Simulation Environment

The simulation environment is a 15 m × 15 m rectangular environment with some number of food tokens (energy sources). Agents can detect another agent or food within a view angle (-90°, 90°) and distance 250 cm. The face of an agent is detected if it is seen within (-75°, 75°) from its front and otherwise its back is visible. A pair of agents can mate if they align their faces within the mating angle (-90°, 90°) and the mating distance 20 cm. Male and female agents have different colors and they can detect each other by the color. The agents can physically interact with each other, which depends on their body size. However, occlusion is not considered. Each generation starts with random positions of the foods and agents in the environment. The total number of foods in the environment is fixed and do not change during simulation experiment. Whenever an agent consumes a food token, the food token disappears from its current position and appears in another random position in the environment. The parameters and variables used in the model are given below.

Table 3.1List of simulation parameters

Parameter	Description	Value
L	Asymptotic body size	Evolving;
α	Growth rate parameter	Evolving;
S	Current Size	Change with time.
S_{Max}	Maximum asymptotic Size	300 cm
S_0	The size at which the size-dependent component of mortality drops to 1/e = 36.8%, relative to its value at size s = 0	≥ 10 cm
M_i	Mortality rate of very large individual	1×10^{-4}
M_d	Mortality rate change with size	1×10^{-5}
E_o	Energy Threshold for growth	40 unit
E_{Max}	Maximum Energy	300 unit
β	Energy cost parameter	0.001
t_{life}	Maximum Lifetime	5000 time steps.
C_R	Reproduction cost (regulates the intensity of sexual selection and sexual conflict)	8- 35 energy unit.
R_{MS}, R_{ME}, R_{FS}, R_{FE}	Parameters of reproduction condition	0.5,0.5,0.5,0.5

3.4 Embodied Evolution Experiment

Each experiment starts with 50 male and 50 female robotic agents. The robotic agents have two layered neural network controller and the genotype consists of 50 real valued genes:

- G(1:48) : The weights of neural network controller.
- G(49) : Growth rate parameter (α).
- G(50) : Asymptotic size (L).

The first 48 genes are the neural network weights, by which the agent take decision which module to choose according to its own sex, energy level, body size, age, and sensory inputs. The next two genes are the growth strategy genes and it affects the input of the neural network containing size information. The sex gene is binary and has value 1 or 0 representing male or female. The initial values of other genes and neural network weights are drawn from a Gaussian distribution with zero mean and standard deviation of 0.1.

The first generation starts with fifty male and fifty female robots. Each agent starts with some initial energy, size and limited lifetime. In their limited lifetime they have to find food to live and find mate for reproduction. Each time step of their lifetime, they loose some energy depending on their body size and growth according to (iv). The agents can gain energy by consuming food, but there is a maximum energy storage threshold, after which even if they consume food, the stored energy does not increase. When agent is in premating state and find a mate (within mating angle and distance) they reproduce according to reproductive condition, where female bears the cost of reproduction C_R, and they produce two offspring (one male and one female). The chromosomes of the offspring's are generated from parent's chromosomes by (one-point) crossover and mutation with probability of 0.001.The offspring's initial size and energy in the next generation is determined by the female's size and energy during reproduction time resembling biological scenario, as maternal phenotype affect offspring quality [45]. When two agents initiate mating they cannot choose other module until they finish mating. After finishing mating, agents turn to post mating state, when they cannot mate for some time. After that they again return to premating state. Agents die either when the lifetime is finished or their energy level become zero or when size dependent mortality condition satisfies. When one generation finishes, rather than taking any explicit fitness function, we take randomly 50 male and 50 female from the offspring to start new generation. As the probability of offspring reproduction depends solely on robotic male and female agent's competing and investing (with size and energy) ability at the mating occasion, the males and females having higher reproductive success has the probability that their offspring inheriting their characteristics has higher chance to survive in the next generation.

3.4 Summary

In this chapter, an embodied evolution model is constructed with intrasexual and intersexual interaction where male and female agents physically meet with each other and exchange genotype to produce offspring for next generation. There are no pre-defined ARTs in the agents (male and female) and they evolve from initially continuous characteristics until convergence. This model displays the three main properties ((emergence from initially continuous characteristics, intersexual and intrasexual interaction, high situatedness with environment)) needed (2.4) to model a full picture of ARTs illustrated in chapter 2.

Chapter 4

Emerged Male and Female ARTs

This chapter reports the result of simulation experiments using the embodied evolution framework described in the previous chapter, which incorporates biological features (vision, body growth, mortality, sex, reproductive cost, limited resource, etc.), where male and female robotic agents naturally face both intersexual and intrasexual interactions for survival and reproduction. Each simulation experiment was run for 700 generations with the population size of 100 agents, where each agent had 5000 time step lifetime. I varied three environmental conditions: food density, reproductive cost and competition level (male-female ratio), to test their effects on the emergence of ARTs. **Figure 4.1** is an example of the evolution of the number of offsprings produced over 700 generations with food density 100, reproductive cost 8 unit, and male-female ratio 50:50.

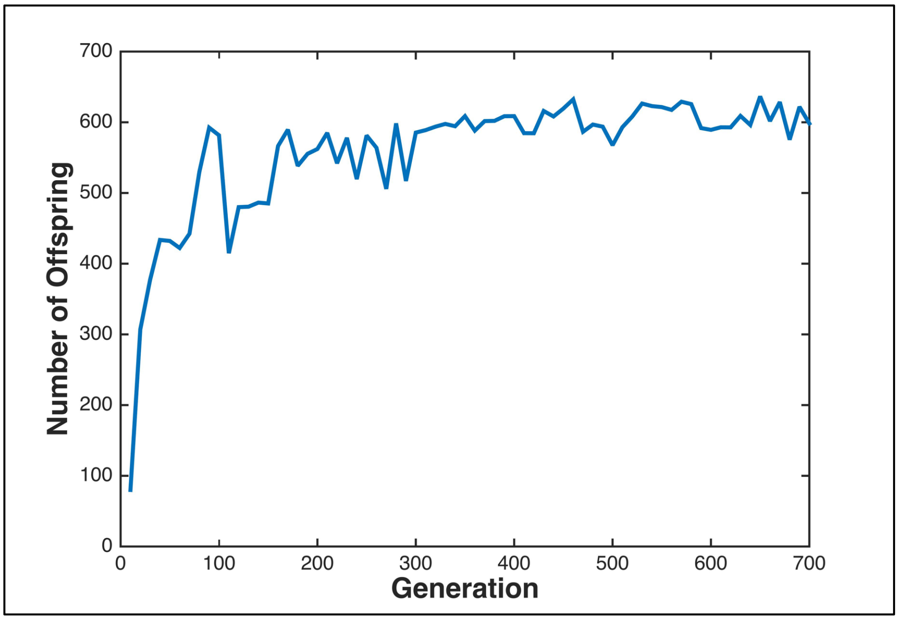

Figure 4.1 The evolution of the number of offsprings in an experiment for 700 generations with food density 100, reproductive cost 8 unit, and male-female ratio 50:50.

For each environmental variable, I considered 6 different points and for each point I repeated 25 simulation experiments. Therefore, for each environmental condition there were 150 total simulated environments. For three environmental conditions, there were total 450 simulated environments. In the following sections, I describe the male and female ARTs found in these 450 simulated environments.

4.1 Male ARTs

Among 450 simulations, male ARTs evolved in 114 simulations. There are three kinds of male ARTs found, which are also closely similar to the ARTs found in nature [2,16,10].

Genetically fixed ARTs: Two types of genetically distinct phenotypes with different tactics emerged in males, dominants and sneakers, that differ in getting access to females. Dominant males increase fitness by maintaining larger body size and being more attractive to female, whereas sneaker males increase fitness following and sneaking females when they come to mate with a dominant male.

Conditional/flexible ARTs: Males evolved to change mating tactics (behaving as dominant or sneaker) according to their body size.

Mixed ARTs: Males of the population evolved to have both fixed and flexible tactics.

In the next section, for each kind of male ARTs, I explain in detail one of the best examples evolved in the simulation environments and describe their properties.

4.1.1 Genetically fixed ARTs

Among the 450 simulations in different environments, distinct phenotypes in male emerged in 57 populations. **Figure 4.2** shows one of the populations with highest fitness (with evolutionary condition: food density 100, reproductive cost 8, male-female ratio 50:50) where male genetically distinct phenotype evolved. A snapshot of the environment (**Figure 4.2 C**) illustrates that there were very large and small males in this population. The male growth curves (**Figure 4.2 A**) show that there was a clearly bimodal distribution in male phenotypes with distinct asymptotic body sizes and growth rates.

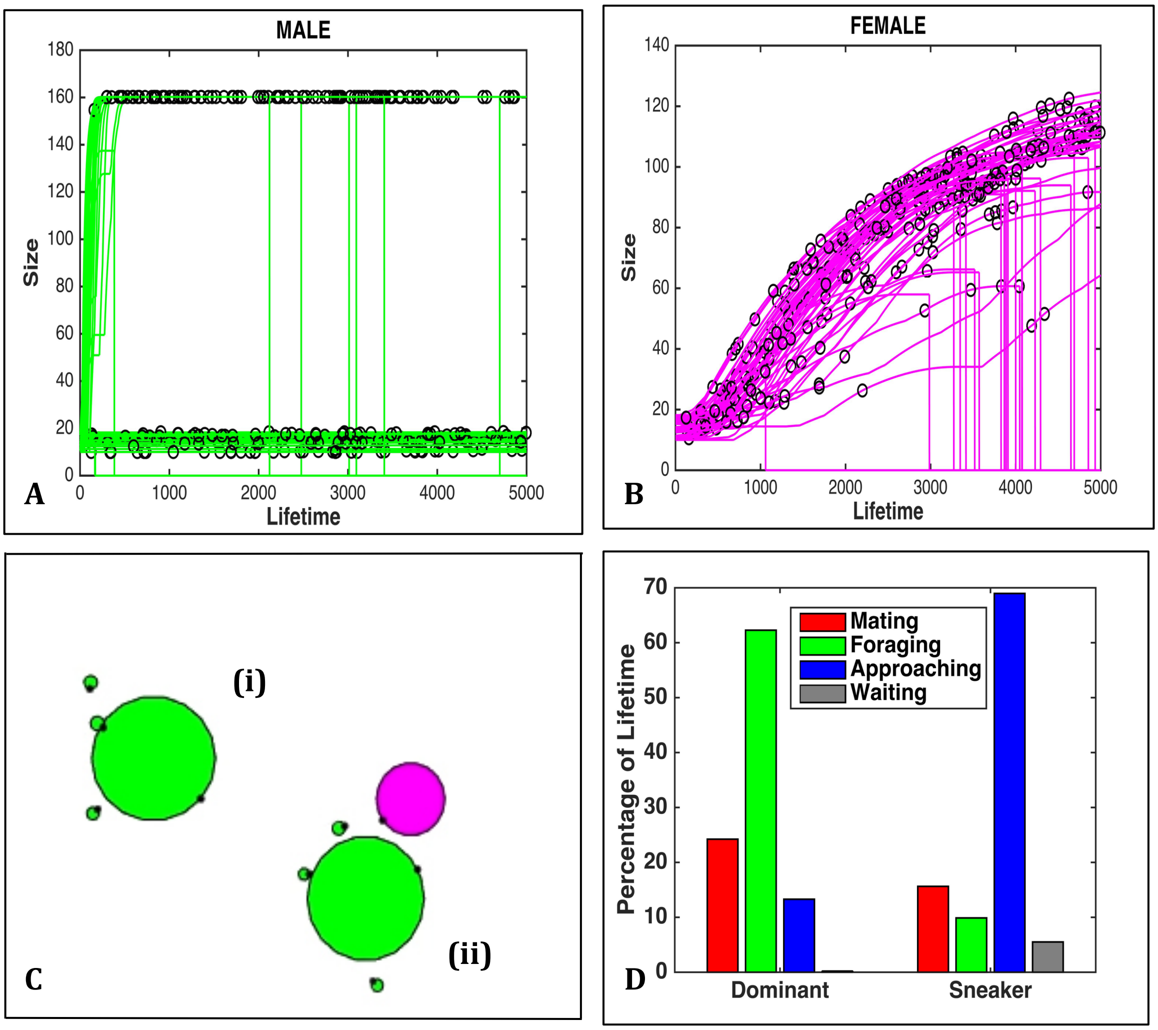

Figure 4.2(A) Growth curve of males in a population where, male ART emerged (black dots denote successful reproduction of offspring) (B) Female growth curve in the population where Male ARTs evolve. (C) Emerged Dominant males (large green), Sneaker males (small green) and Females (pink). (i) Sneaker males flock around a Dominant. (ii) One Female came to a Dominant male, which is an opportunity for sneaker males to mate. (D) Dominant and Sneaker males' average behavior choice in their lifetime.

I define the phenotype with the body size larger than 150 cm (for this population) as a dominant male and the phenotype with the body size under 25 cm (for this population) at the end of the lifetime as a sneaker male.

This type of dominant-sneaker male ARTs are 'fixed', which means the dominant and sneaker males never change their behavior throughout their lifetime. **Figure 4.2 D** shows the average choices of behavioral modules by dominant and sneaker males throughout their lifetime.

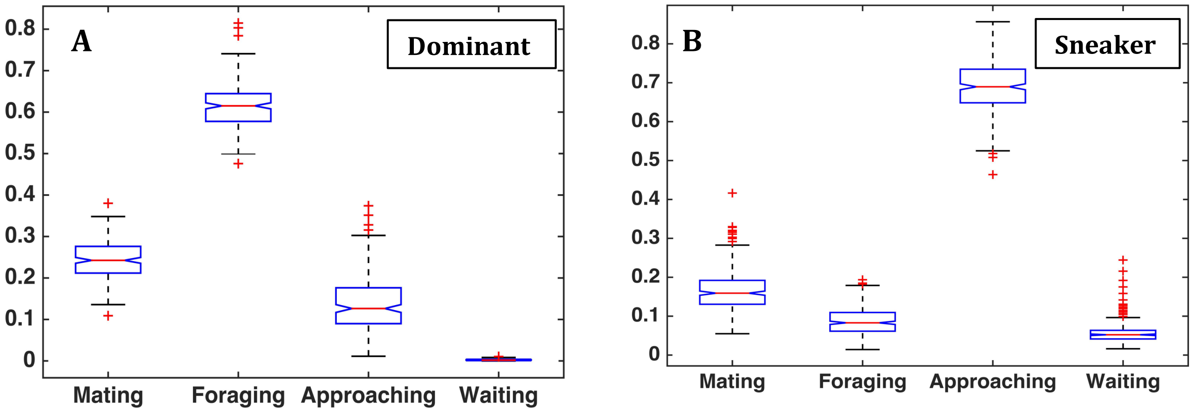

Figure 4.3 Kruskal-Walis test (box plot visualization) of behavioral module choice of dominant (A) and Sneaker (B) males.

To test if the mean of the lifetime invested for each module are significantly different, dominant and sneaker males' module choice information of last 10 generation is taken, and Kruskal-Wallis statistical test is performed (as the data are not normally distributed). Figure 4.3 shows the Kruskal-Wallis test box plot. It is found that-

- For dominant males (Figure 4.3A), the null hypothesis that the choices of behavioral module come from the same distribution was rejected at 1% significance level. It is statistically significant that dominant males invested longest time in foraging module.

- For sneaker males (Figure 4.3B), the null hypothesis that the choices of behavioral module come from the same distribution was rejected at 1% significance level. It is significant that sneaker males invested longest time in approaching module.

The results confirm that dominant males spent longest time for foraging and maintain larger body size, which is important to win competition for getting access to female, and that sneaker males spent most of their time for approaching to follow dominant males or females [2,16].

Analysis of Behavior and Genotype

To investigate the interactions of male and female behaviors, we took the highest fitness population with distinct male ARTs and analyzed their behaviors of dominant and sneaker males in specific situations with a female, summarized in **Figure 4.4.**

- When only female face visible: While dominant males initiate mating or look for food depending on energy, Sneaker males always approach towards female.
- When only female back visible: While dominant males always forage for food, sneaker males always initiate mating.
- Female face visible in mating distance (0.2 meter) when food visible: While dominant males initiate mating or approaching depending on own energy, sneaker males always approach towards male or female.
- Female back visible in mating distance (0.2 meter) when food visible: While dominant males always go for food, sneaker males always initiate mating.

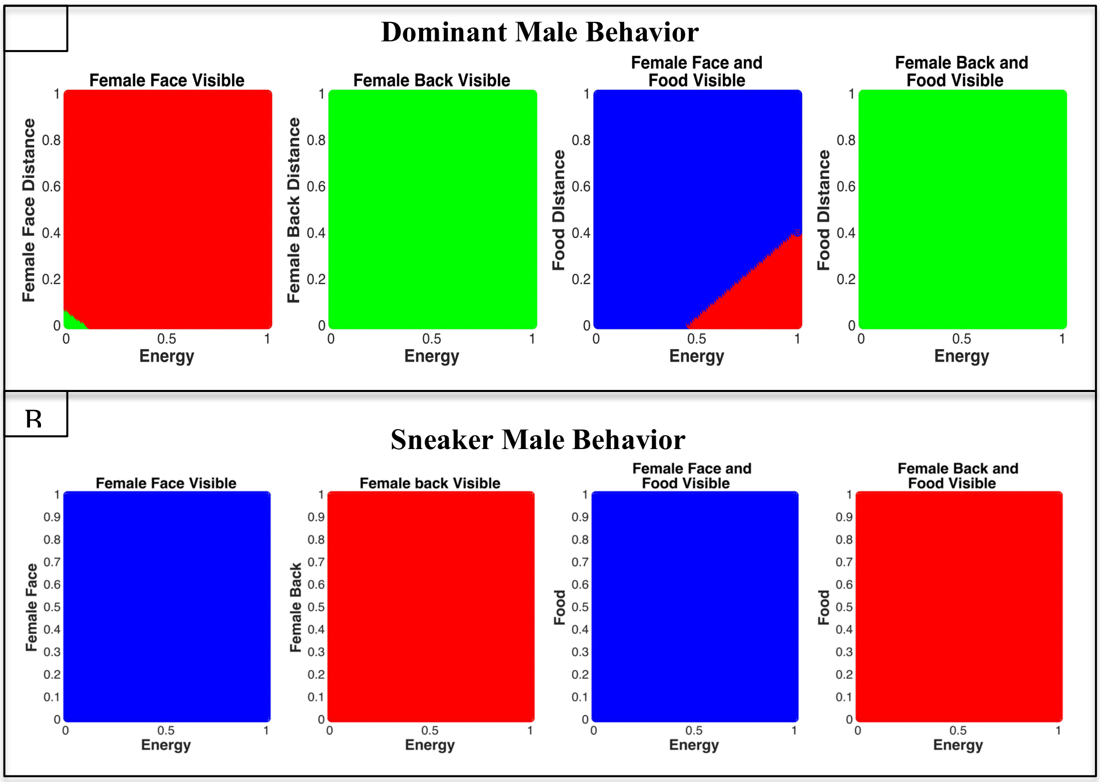

Figure 4.4 Behavior of Dominant male (A) and Sneaker male (B). Red:Mating;Green:Foraging,Blue:Approaching

Dominant males choose mating module when female face is visible. When female back is visible, they prefer to look for food rather than following female. When a female is visible along with another male, dominant males choose approaching and mating to push away small males to get access to female, as they have large body size.

Sneaker males always tend to mate from female back. A male sees a female's back when the female face angle is greater than 75°. For successful mating, a male have to align its face with female face within 90° (Chapter 3, Section 3.3). Therefore to mate from a female's back, a male approach the female within narrow (90-75=15)° angle from the side. Sneaker males tend to mate from this narrow angle on the side of a female.

When sneaker males see female face and another male, they choose approaching or following module, which leads them to cluster around dominant male and flock together. But when sneakers see female back along with another male they initiate mating which helps them to sneak females who come to initiate mating module with dominant males. This behavior of sneaker male can depend on female behavior.

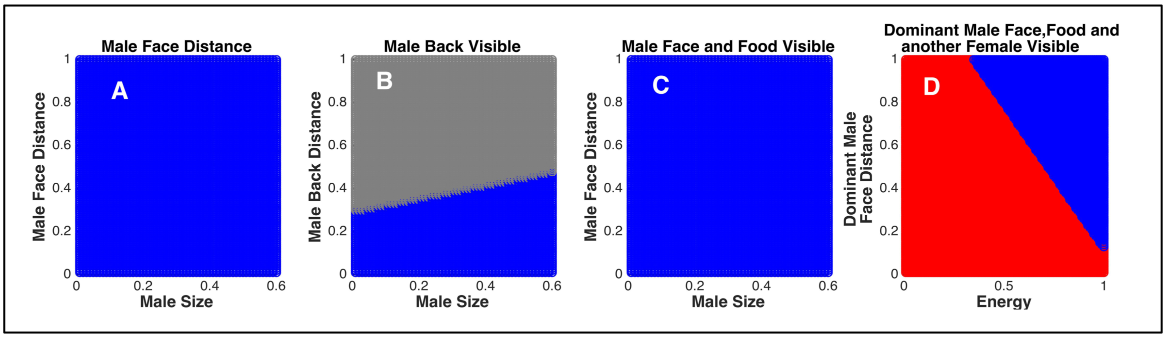

Figure 4.5 Behavior of females with male ARTs;
Red:Mating;Blue:Approaching and Gray:Waititng

As female behaviors can depend on the body size of the nearest male, they can behave differently with dominant or sneaker males, which can shape alternative behaviors of males. To clarify how females interact with dominant or sneaker male, we analyzed how females react to them in different situations, as illustrated in **Figure 4.5**.

- Male face visible: Always approach towards male of any size.
- Male back visible: Either wait or approach toward male depending on the body size of the closest male.
- Male face and food visible (0.2 meter): Always approach towards male.
- Dominant male's face, food (0.2 meter) and another female visible: Initiate mating or approach towards dominant male when it is far.

Approaching behaviors of females work differently for dominant and sneaker males. When a female collides with a sneaker male, she can push back or chase them away as a sneaker male's size is smaller than the female's. As dominant males are bigger than females, when a female approaches, she stays near the dominant male. This is what females do when male face is visible (**Figure 4.5 A and C**). When male back is visible (**Figure 4.5 B**), females tend to follow larger size males by taking approach behavior. When there is a male face and another female visible (**Figure 4.5D**), females choose to approach larger males at a distance and initiate mating when the distance reduces. This leads females cluster around dominant males. It is clearly seen that females are preferring to mate with dominant males and as a result, sneaker male evolved the behavior to mate female from back or sneak when female come near dominant male.

We further analyzed if dominant and sneaker males are clearly genetically different. **Figure 4.6** shows the histograms of the input weight genes for the four behavioral outputs of the males. The genotypes are clearly divided into two groups.

From these analyses of their phenotypes and genotypes, dominant and sneaker male are characterized as follows.

1) Dominant males have high growth rate (α) and large body size, which incur high growth cost (Chapter 3, equation (*iv*)), and invest more of their time to look for food to maintain their large body size. They can get less interruption during mating (win the competition to get access to the female) and increase their fitness (chance of getting offspring). They prefer mating from female face, as females tends to move towards larger males for mating.

2) Sneaker males have low growth rate (α) and small body size, which incur low growth cost, and invest most of their time looking for and following female to mate. As they cannot win a competition with a dominant male by approaching a female, they follow and flock around a dominant male and, when a female comes near and choose mating, they sneak mate with the female. Sneaker males prefer mating from female back as females can easily chase away small size sneakers if they try to initiate from the front.

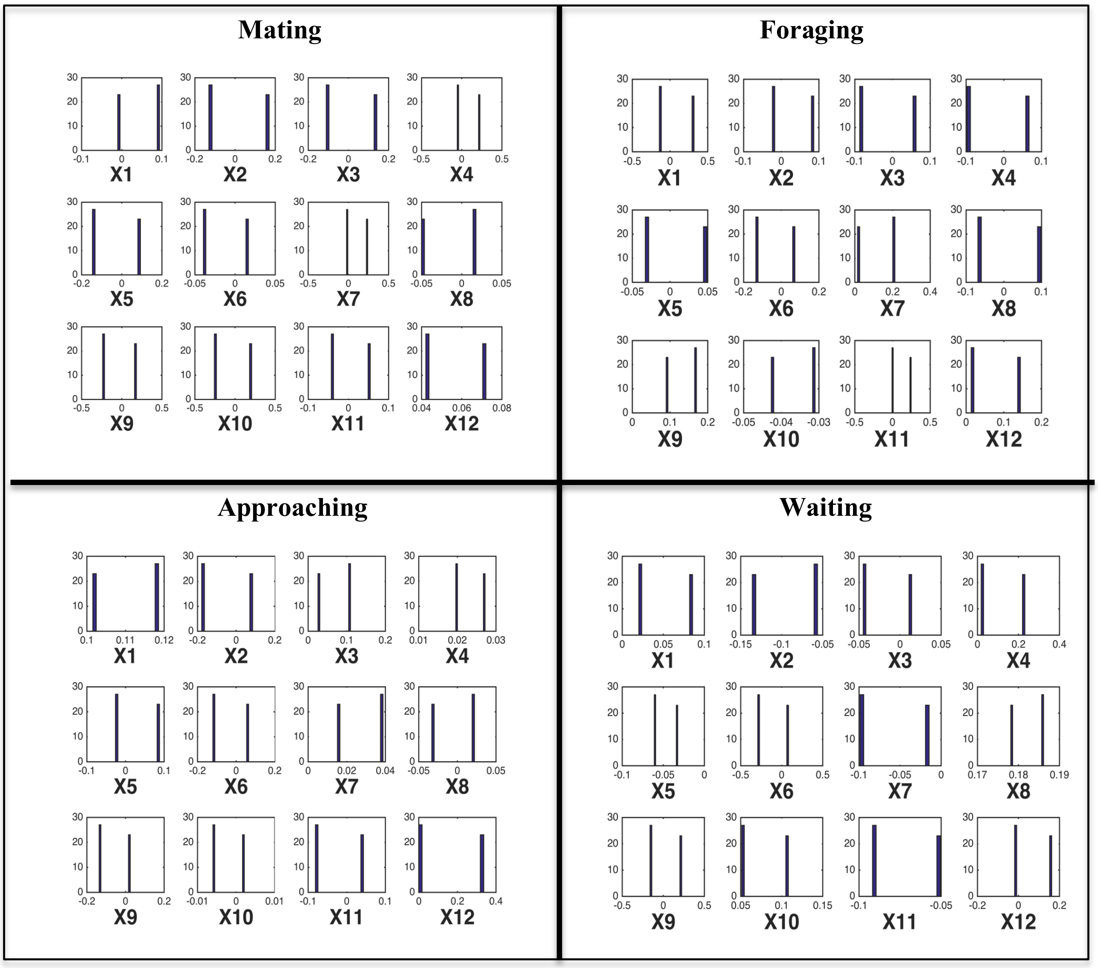

Figure 4.6 Histogram of 12 neural network input weight genes of all four module. The tall bars correspond to the sneaker males' genes and the short bars to the dominant males' genes, showing distinct distribution in genotype.

4.1.2 Conditional or flexible ARTs

If Individuals switch between tactics according to certain conditions or growth, then it is referred as 'flexible or conditional ARTs'. In our simulation experiments, among the 450 populations evolved in different environments, there were 55 populations where males evolved to choose different tactics depending on a condition, which was the body size.

Figure 4.7 illustrates one of the populations with highest fitness (with evolutionary condition: food density 200, reproductive cost 8, male-female ratio 50:50) where male conditional ARTs evolve. **Figure 4.7(C)** shows the growth curves of the males and it is seen that they don't have distinct subtypes like in genetic ARTs. The black circles on the growth curves show successful mating, which happened in a wide range of body size. The gene histograms for the mating module in **Figure 4.7 (D)** shows that there were no distinct subgroups in genotypes, which was the case for all other genes as well. Therefore, this population was genetically undifferentiated.

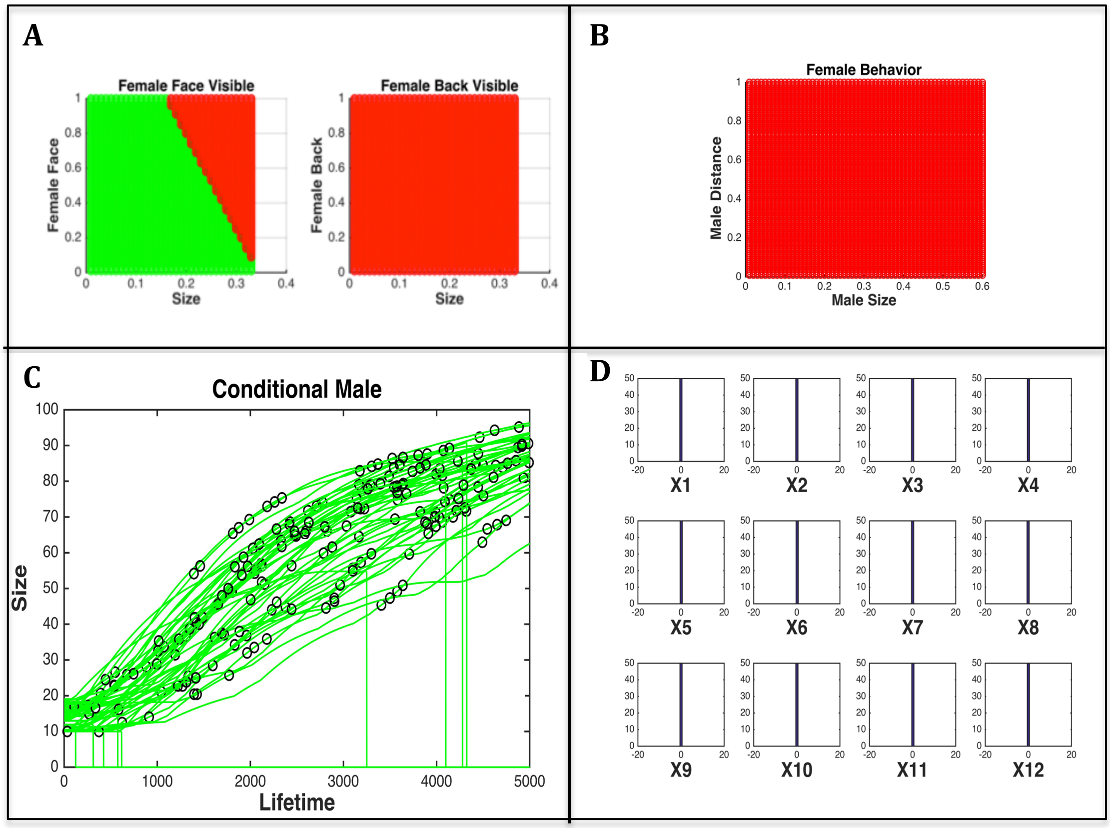

Figure 4.7 (A) Behavior of Conditional ART in males. Red:Mating; Green:Foraging, Blue:Approaching. (B) Female behavior when a male is visible. Red:Mating. (C) Growth curve of males in a population where, conditional ART emerged (black circles denote successful reproduction of offspring). (D) Histogram of 12 neural network input genes of mating module.

Figure 4.7 (A) shows how the males behaved with a female depending on their body size:

- When a female face visible: A male looks for food when it is smaller than 0.15 (45 cm), but chooses mating when it is larger than 0.15 (45 cm).
- When a female back visible: A male of any size initiates mating.

From these behaviors, it is seen that males mate from female’s back like sneakers (illustrated in section 4.1.1) while their body size is smaller than 45 cm. And when males grow larger than 0.15 (45 cm), they start mating from female’s face as dominant males (illustrated in section 4.1.1). Therefore, the males change their mating tactic according to their body size condition and they are defined as conditionally flexible males. **Figure 4.7(B)** shows the behavior of females when a male is visible. Females always choose mating for males of any size. Although females don't choose males according to quality (size), females can easily chase away or avoid small males when they are not interested in mating. Also, relatively larger males can move away smaller males to access female. Therefore, being sneaker at small size gives male the opportunity to increase fitness by mating from back and also avoiding the competition to accessing female.

4.1.3 Mixed ARTs

When there is a fixed and flexible tactic both seen in the mating behavior, then it is called mixed ARTs. Mixed ARTs are rare phenomenon in nature. In our simulation experiments of 450 populations in different environments, male mixed ARTs evolved in only two populations with low reproductive cost (cost =8,10 unit) and medium (100,150 unit) food density

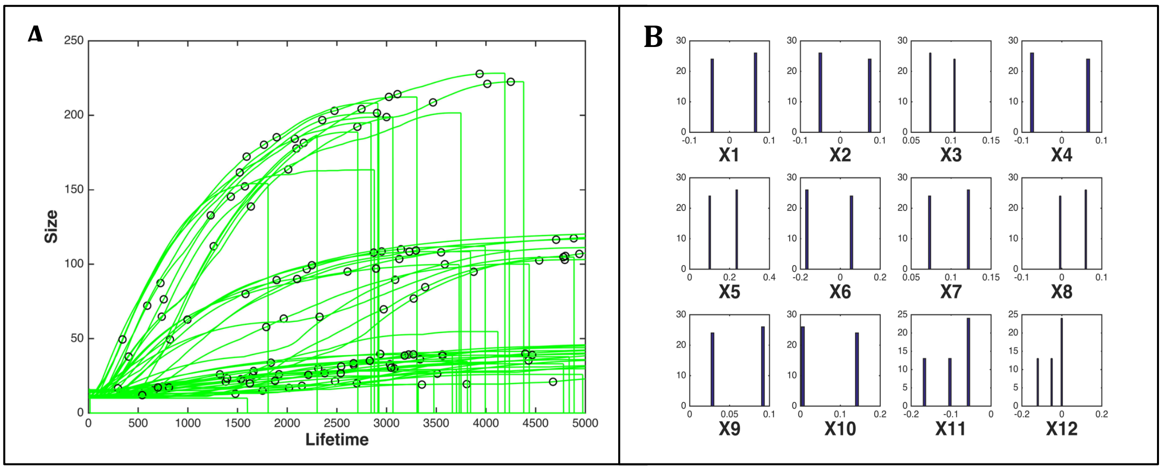

Figure 4.8(A) Growth curve of males when mixed tactics evolved. (B) Histogram of 12 neural network input genes of mating module.

Figure 4.8(A) illustrates the male growth curves for the population with evolutionary condition: food density 100, reproductive cost 8, and male-female ratio 50:50. The males with the lowest size and growth rate behave as sneaker males (section 4.1.1). The males with the highest size and growth rate act as conditional males (section 4.1.2), who perform mating both when they are small and large (black circles). The males with higher size and growth rate than sneaker, but lower size and growth rate than conditional males behave as dominant males (section 4.1.1), who perform mating only when they are grown up.

Therefore, the population consisted of three ARTs:

i) Dominant male
ii) Sneaker male and;
iii) Conditional male.

The genotype histogram **Figure 4.8(B)** shows that the genotypes for mating in the mixed ARTs are clearly divided into three groups for input X_{11} (distance to the female back) and X_{12} (distance to the food), which are relevant for the sneaker tactic. Other genes, dominant and conditional males shared the same genotype, showing only two distinct genotypes.

4.2 Female ARTs

Among the 450 simulations in different environments, distinct phenotypes in female emerged in 27 populations. The phenotypes differed in their offspring quality and quantity. QoFs (Quality oriented females) produced lower numbers of higher quality offspring, whereas NoFs (Number oriented females) produced higher numbers of lower quality offspring. This kind of female ARTs are also found in nature [20,21]. Next I explain in detail one of the best example of the female ARTs found in the simulation environments and describe their properties.

Figure 4.9 shows one of the populations with the highest fitness where female distinct phenotype evolved (with evolutionary condition: food density 100, reproductive cost 8, male-female ratio 50:50). The female growth curves (**Figure 4.9 A**) show that there was a clearly bimodal distribution in the female phenotypes with asymptotic body sizes and growth rates. Among 50 females, 16 of them were larger than 130cm and 34 of them were smaller than 70 cm at the end of their life.

The male and female growth curves (**Figure 4.9 A) and Figure 4.9 B)** in the population reveals that the initial size of the both males and females had two subgroups. **Figure 4.9 C** illustrates the behaviors of the females. When a male and food are visible, larger females

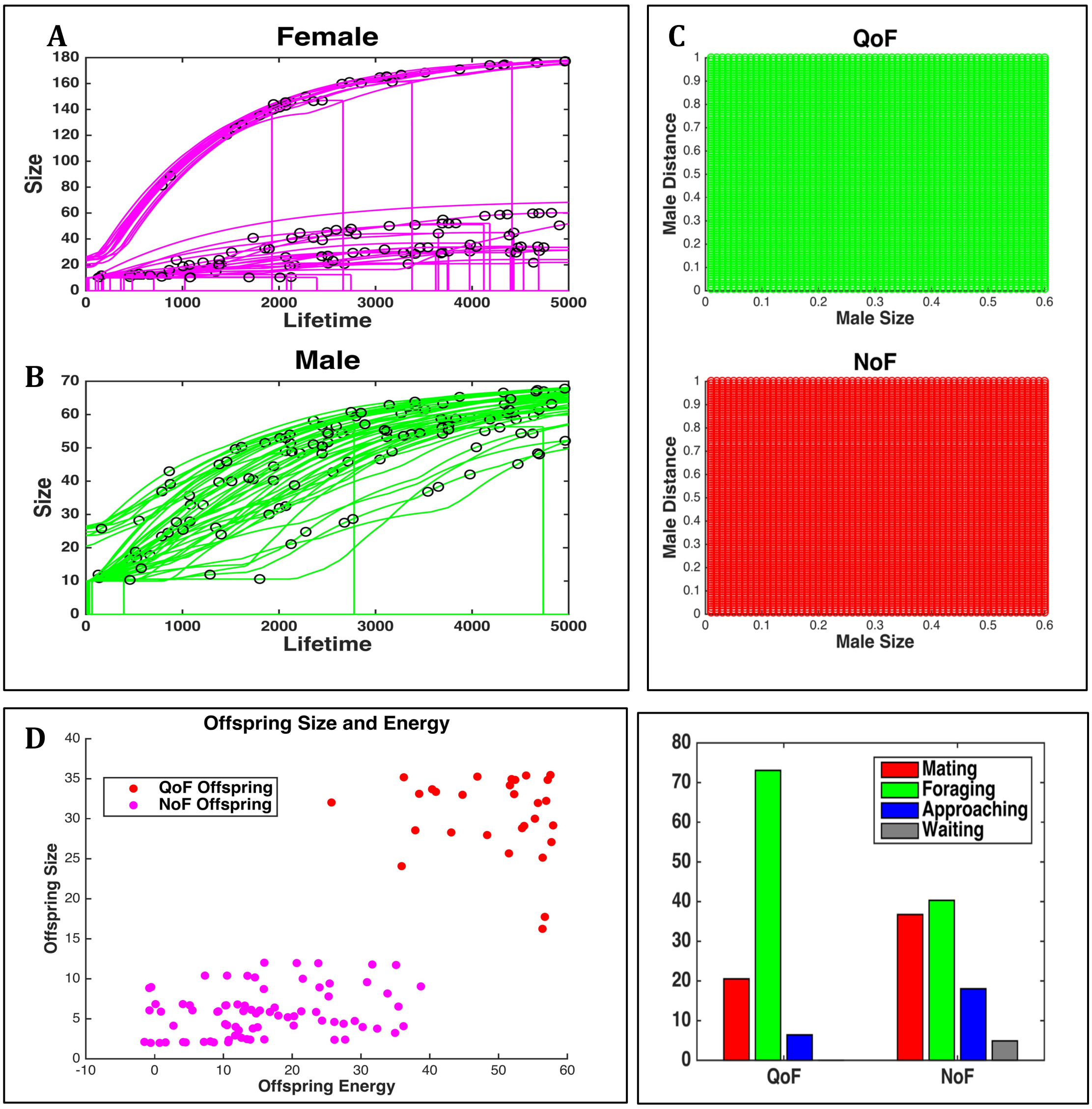

Figure 4.9 Growth curve of female (A) and male (B) when female ARTs emerge in the population. (C) QOF and NOF female behavior when Male face and food visible. Red:mating; Green:Foraging. (D) Offsprings' size and energy of QoF and NoF.

always go for food and smaller females always initiate mating. **Figure 4.9 D** shows the size and the energy level of the offspring at birth, which depended on the size and the energy level of the mother at the time of mating (see section 3.1.1)**,** Thus the smaller females produce many small size, low energy offspring and larger females produce fewer large size, high energy offspring. **Figure 4.9 E** shows the average (mean) choices of behavioral modules by larger (QoF) females and smaller (NoF) females throughout their lifetime.

To test if the mean of the lifetime invested for each module is significantly different, QoF and NoF females' module choices in the last 10 generations were taken and Kruskal-

Wallis statistical test was performed (as the data were not normally distributed). Figure 4.10 shows the Kruskal-Wallis test with the box plot. It was found that-

- For QoF females (Figure 4.10A) - the null hypothesis that the choices of behavioral module come from the same distribution was rejected at 1% significance level. The QoFs invested significantly longer time in foraging than in mating.
- For NoF females (Figure 4.10B) - the null hypothesis that the choices of behavioral module come from the same distribution was rejected at 1% significance level. The NoFs invested significantly longer time in foraging and in mating.

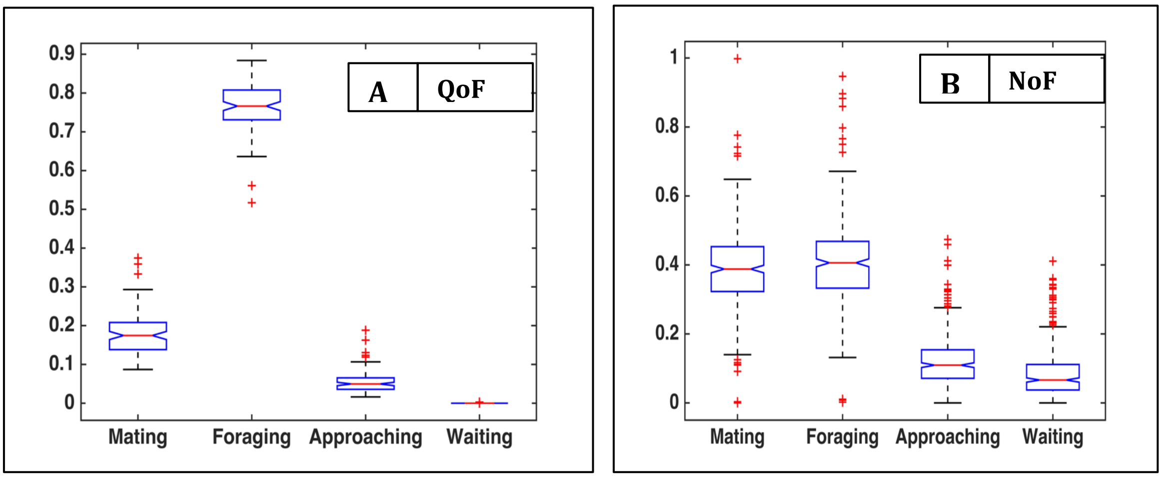

Figure 4.10 Kruskal-Walis test (box plot visualization) of behavioral module choice of QoF (A) and NoF (B) females.

From the findings above, the larger and smaller female phenotypes are characterized as follows.

1) Quality oriented female (QoF): QoFs are large in size, less interested in mating, and produce small number of high quality (large and high energy) offspring.

2) Number oriented female (NoF): NoFs are small in size, highly interested in mating, and produce a large number of low quality (small and low energy) offspring.

As the offspring's initial size and energy depend on the maternal size and energy, rather than competing to get access to mate, females can compete in their offspring quality and quantity. When male and food are visible, QoFs always choose to forage to produce more quality offspring. On the contrary, NoFs always choose to go for mating to produce as many offspring as possible.

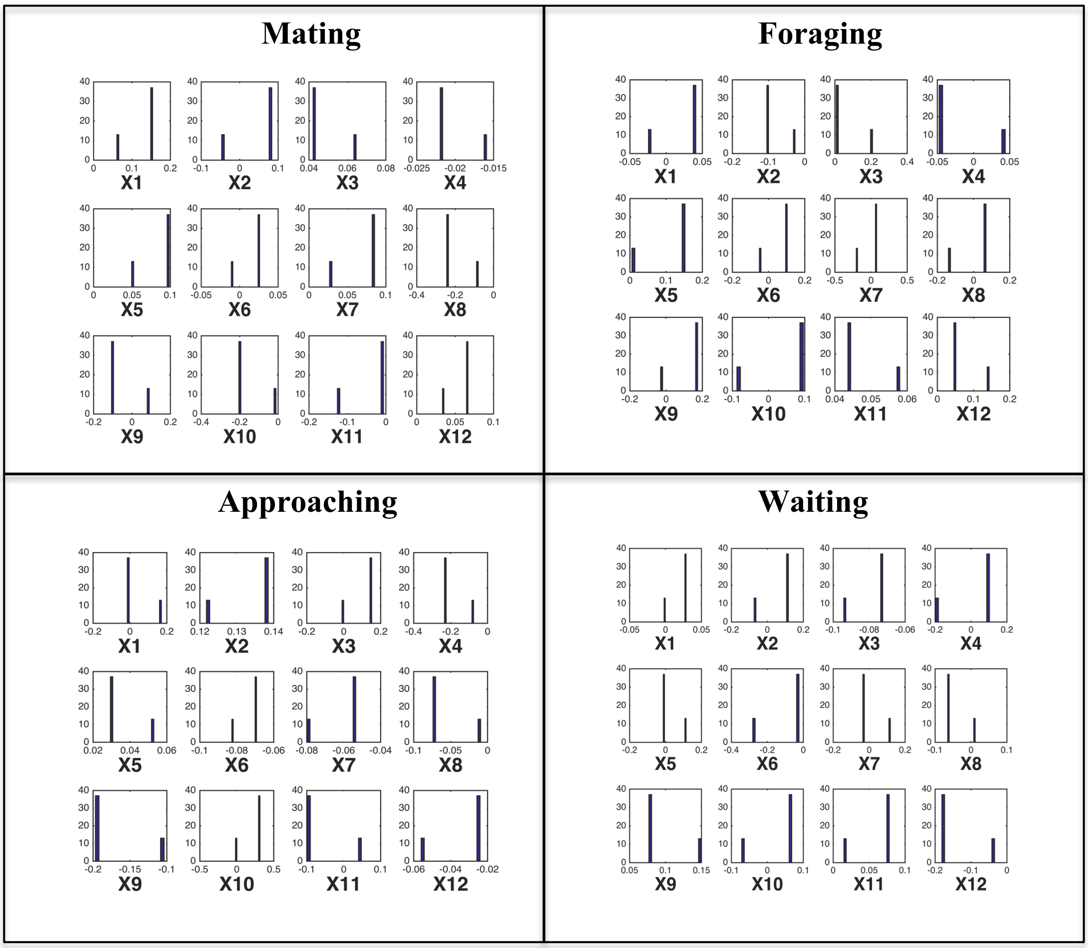

Figure 4.11 Histogram of 12 neural network input genes of four modules. The tall bar is the QOF's genes and the short bar is the dominant NOF's genes showing distinct distribution in genotype.

It is also found that QOFs and NOFs are clearly genetically different **(Figure 4.11)**. For each behavioral module, the histograms of all genes were clearly divided in two groups.

4.3 Male and Female ART's fitness curves

Figure 4.12 shows the fitness curves of the populations (with food density 100, reproductive cost 8 unit, and male-female ratio 50:50), where male fixed ARTS (4 populations), male conditional ARTs (6 population), male mixed ARTs (1 population) and female ARTs (3 populations) evolved, along with those of the populations (11populations) where no ARTs evolved.

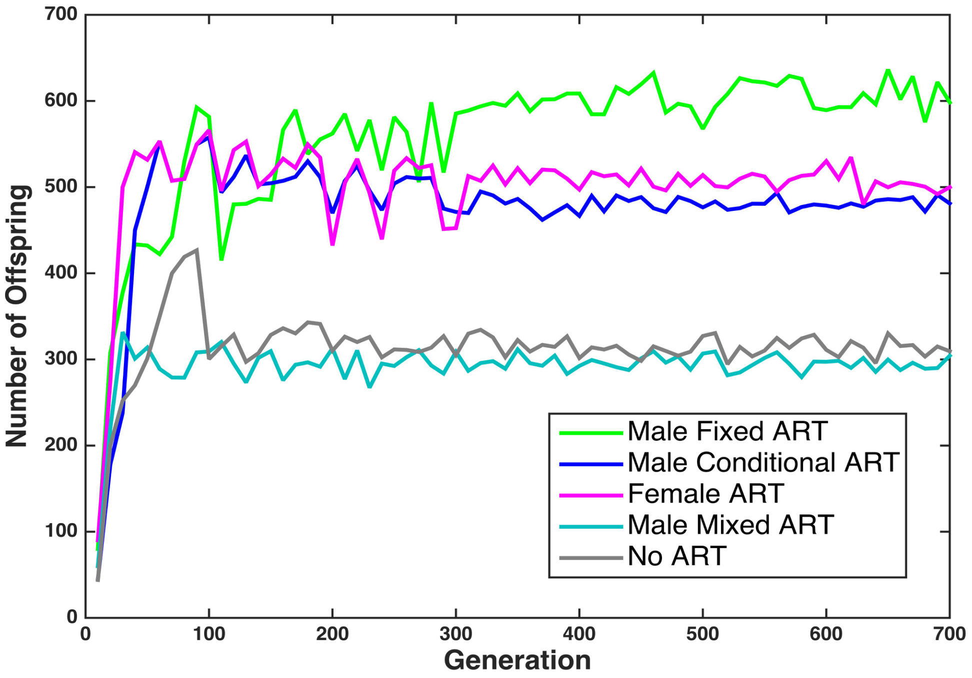

Figure 4.12 Fitness curves of the population (with food density 100, reproductive cost 8 unit, and male-female ratio 50:50) where male or female ART evolved.

The population with male fixed ARTs converged to the highest fitness. The population with male conditional ARTs had slightly lower fitness than that with male fixed ARTs, and the population with male mixed ARTs had much lower fitness than Male fixed and conditional ARTs. The population with female ARTs had fitness closer to male conditional ARTs. To test if the fitness of the population with male (fixed, conditional) ARTs, female ARTs and no ARTs significantly different statistical t-test is performed and it is found that-

- For male fixed ARTs- the null hypothesis that the fitness of population with male fixed ARTs and no ARTs came from the same distribution was rejected at 5% significance level. The populations where no ARTs evolved had significantly lower fitness than the populations where male fixed ARTs evolved.
- For male conditional ARTs- the null hypothesis that the fitness of population with male conditional ARTs and no ARTs came from the same distribution was rejected at 5% significance level. The populations where no ARTs evolved had significantly lower fitness than the populations where male conditional ARTs evolved.

- For male mixed ARTs- the null hypothesis that the fitness of population with male mixed ARTs and no ARTs came from the same distribution was not rejected at 5% significance level. The populations where mixed ARTs evolved had lower but not significantly different fitness than the populations where no ARTs evolved.
- For female ARTs- the null hypothesis that the fitness of population with female ARTs and no ARTs came from the same distribution was rejected at 5% significance level. The populations where no ARTs evolved had significantly lower fitness than the populations where female ARTs evolved.

The statistical test shows that, the population where no ARTs evolved had lower fitness than the populations where male fixed, male conditional and female ARTs evolved. Therefore in this environment, rather than converging to the same tactic, agents evolved to choose alternative tactics to gain higher population fitness. The populations where mixed male ARTs evolved had lower but not significantly different fitness than the populations where no ARTs evolved. The number of mixed ARTs also evolved in negligible number (only one time) in the simulation environments.

4.4 Summary and Main Findings

In this chapter, the evolution of ARTs are analyzed with representative example populations. Male and female ARTs evolved from initially monomorphic populating in an embodied simulated robot evolution framework (Chapter 3) with intersexual and intrasexual interactions. In the evolved genetically fixed male ARTs, dominant and sneaker tactics are quite similar to the tactics observed in males in all major taxa [2,16,10], commonly called as investor or dominant and exploiter or sneaker. The conditionally flexible males who changed mating tactic according to their body size, which were found in the simulation, are also quite common [3,16,9], especially in animals having indeterminate growth [2,16]. The mixed ARTs in males [41,8] are rare compared to the fixed and flexible tactics in animals. Similarly, mixed ARTs emerged only in a small number of populations in our simulation. In the environment shown in Figure 4.12, male fixed and conditional ARTs had higher fitness than the populations without ARTs. On the other hand, the fitness of male mixed ARTs was lower but not significantly different than the no ART populations, which explains why mixed ARTs was found in negligible number than other ARTs in our simulation.

Female ARTs are much less studied than male ARTs and they usually differ in their quantity of mates [20,21], mate conflict or coercion [22,23], and investment for eggs or fecundity [24,25,26]. The evolved female ARTs (QoF and NoF) in the simulation environment are also quite similar to those found in nature. One of the best examples could be the female of side-blotched lizard, studied by Sinervo et al [110]. Orange throated female-produce high quantity offspring and yellow-throated female-produce high quality offspring, which are quite similar to NoF and QoF emerged in our simulation.

Chapter 5

The Effect of Environmental Conditions on Male and Female ARTs

In the previous chapter, I have described the evolved genetically distinct, conditional and mixed male and female ARTs. This chapter I will discuss how the male and female ARTs evolved in different environmental condition. I consider three key variables of environmental conditions – food density, reproductive cost, and male-female ratio. For each environmental condition, I test 6 levels and for each level I repeat 25 simulation experiments. Therefore, for each environmental condition, there are 150 total simulated environments, where hundred male and female agents evolved for 700 generations with 5000 time step lifetime. For three environmental conditions there were in total 450 simulation environments, where Male ARTs were observed in 112 environments (57 genetically distinct ART, 55 Conditional ART and 2 mixed ART) and Female ARTs were observed in 27 environments.

To understand the effect of environmental condition I will measure five properties for each condition (food density, reproductive cost, and male-female ratio)-

1. Number of populations where male and female ARTs evolved.
2. Percentage of population with only Dominant or Sneaker males evolved.
3. Percentage of population with only QoF or NoF females evolved.
4. Percentage of population with choosy females. Females are defined choosy if they are more interested more to high quality (larger) male than low quality (smaller) males. **Figure 5.1** gives an example where a male is visible to a choosy female. When nearest male has lowest size (10 cm) , female approaches towards male until male distance is, D_{ms}=70 cm. When nearest male size is highest(180 cm), female approaches toward male until male distance is D_{mb}=250 cm. Therefore, female follows larger male from longer distance, which makes it to go towards or choose

larger male more than smaller one. I define female choosy if, $D_{ms} - D_{mb}$ is greater than threshold δ=50cm.

In **Figure 5.1**, $D_{ms} - D_{mb}$=(250-70)=180 cm >δ. So it is defined as choosy.

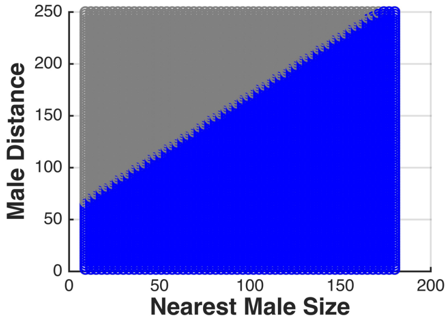

Figure 5.1 Behavior of Choosy female. BLUE: approaching module; Ash waiting

5. Average lifetime invested by male and female for mating (LIM).

The next sections I am going to describe in detail the result for each environmental condition.

5.1 Food Density

Male and female has to capture food not only to live but also to maintain body size. To understand how food density affects the emergence of male and female ARTs, I took 6 different food densities with the number of food source (20, 50, 80, 100, 150, 200) in the environment while fixing the reproductive cost (8 energy unit) and the male female ratio 50:50. For each food density, 25 sets of simulation were performed. In total 150 sets of simulations, male ARTs were found 49 times (20 fixed ARTs, 29 conditional ARTs) and female ARTs 18 times.

Figure 5.2 illustrates the result of different food density test-

- Figure 5.2(A): the number of Male and Female ARTs evolved in different food density is shown. Male fixed ARTs evolved in 3 to 4 times in 25 experiments with all food densities. In contrast, male conditional ARTs increased as food density was increased and stayed 7 out of 25 for 100 and higher densities. Female ARTs also depended on food density. The number of female ARTs was highest (6 times) at low food density and it decreased as food density was increased.

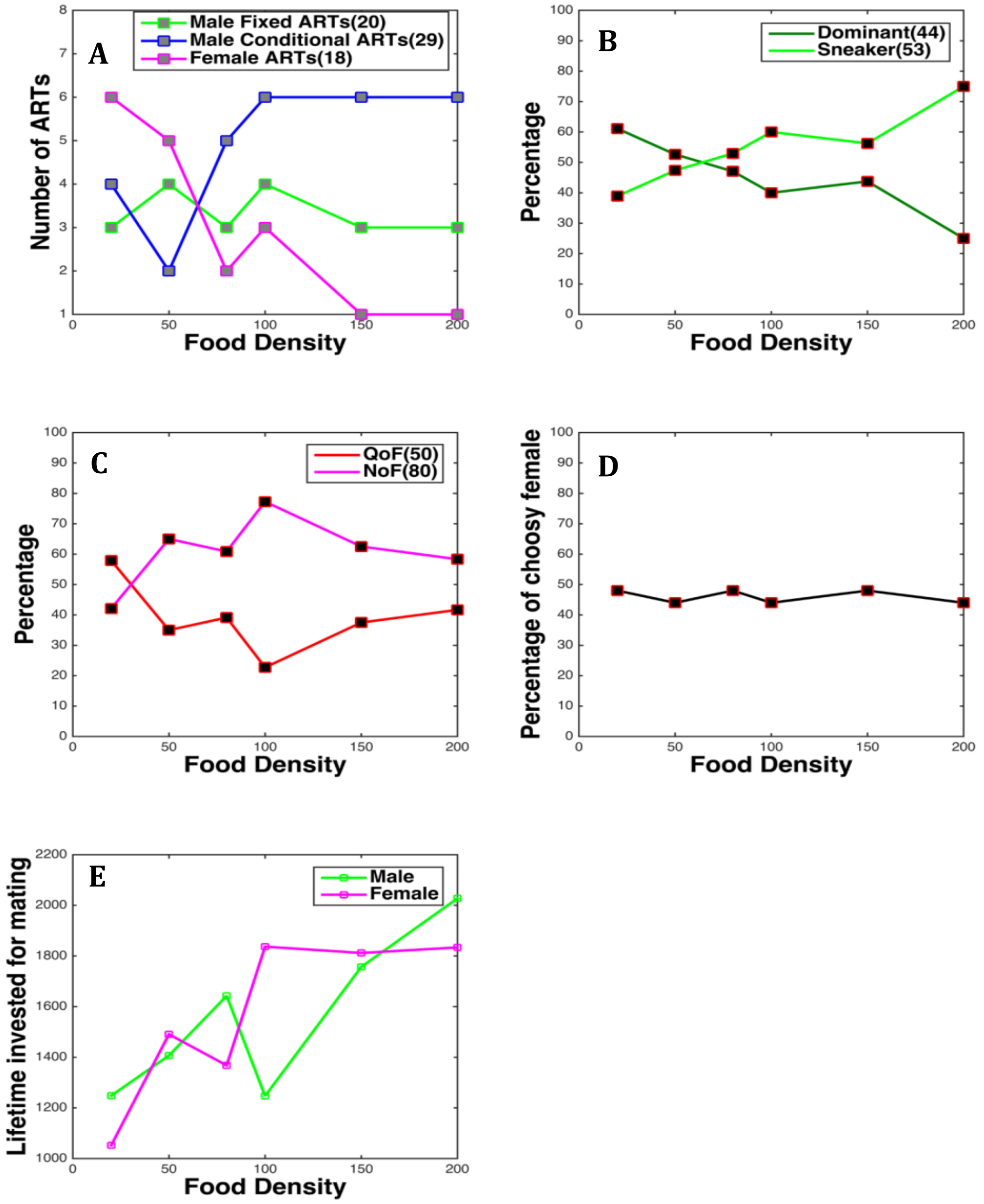

Figure 5.2 Effect of Food Density on Male and Female ARTs. (A)Number of Male fixed ARTs (fixed (20) and conditional (29)) and Female ARTs (18) emerged. (B) Percentage of Dominant and Sneaker males in the populations (97 out of 150) where male ARTs not emerge. (C) Percentage of QoF and NoF female in populations (130 out of 150) where female ARTs not emerge. (D) Percentage of population with choosy female emerged out of 150 population. (E) Lifetime investment for mating (LIM) of male and female.

- Figure 5.2(B): The percentage of Dominant and sneaker males when male ARTs did not emerge (evolved populations of 97) in different food density environment is shown, In the case when male ARTs did not emerge, the proportion of sneaker males increased from 40% to 75% as food density was increased.
- Figure 5.2(C): The percentage of QoF and NoF females in the environments where Female ARTs did not emerge (evolved populations of 130). The proportion of (evolved populations with) quality oriented females decreased up to food density 100, but increased as food density was further increased.
- Figure 5.2(D): The percentage of evolved population consisting choosy female. The percentage of choosy female vary around 50% for all food density, which illustrates that, the intensity of sexual selection (female's tendency to choose male according to their quality) is about same in all food density.
- Figure 5.2(E): Average lifetime invested by male and female for mating in the final 10 generation of 25 repetitions and then averaging the results. Although male lifetime investment for mating (LIM) increased with food density, female LIM plateaued above food density 100.

Male ARTs

As females can choose mating partner (with the male quality seen) to increase their reproductive success, males always compete with each other to get access to female. The dominant and sneaker males (explained in Chapter 4) differ in their tactic of accessing female and also in choice by female. With increased food density, percentage of populations (Figure 5.2D) evolving choosy female don't vary much. This illustrates, female choice according to male quality (size), that is, the intensity of sexual selection is about similar in all food density environments. As a result, the number of male fixed ARTs evolved is also about similar for all food density. Conditional ARTs increased significantly when males' LIM also reaches to highest which leads to reduce competition for accessing female. As male competition to access female decrease, rather than fixed ARTs (extreme dominant and sneaker), conditional ARTs get higher success and emergence of conditional ARTs increase. However, the result of Figure 5.2A shows that, male conditional ARTs evolved in higher number in higher food density and more sensitive to low competition level than low intensity of sexual selection. On the other hand, male fixed ARTs are mainly sensitive to the intensity of sexual selection.

Female ARTs

Female ARTs reduced when food density was increased (Figure 5.2A). A potential reason is the carrying of reproductive cost by females. As female ARTs (explained in chapter 4) evolved as quality oriented (increase offspring quality) or quantity (number) oriented (increase offspring number), when food is scarce and not always available, females face high trade off to invest in offsprings by either increasing quality (capturing more food) or quantity (increased mating). When food density is increased, food becomes always available to females and the tradeoff reduces, which may reduce female ARTs.

With increased food density, females' lifetime investment in mating (LIM) increase (Figure 5.1E) and the proportion of NoF increase (Figure 5.1C). But when food density reaches 100, the same as the population density, the lifetime investment for mating doesn't increase any more although food density is increased. When there is more than one food per individual available in the environment, females may concentrate on increasing offsprings' quality, which may increase the percentage of QoF.

5.2 Reproductive Cost

The assumption in this experiment is that the reproductive cost is the energy incurred by females for successful reproduction. To understand how reproductive cost affects the emergence of male and female ARTs, I took 6 different levels of reproductive cost (10, 15, 20, 25, 30, 35) in the environment with fixed food density (100 foods) and male ratio (50 males). For each level of reproductive cost, 25 sets of simulation were performed, where male ARTs were found for 29 times (14 fixed ARTs, 15 conditional ARTs) and female ARTs for 5 times in the evolved generation out of 150 simulations in total.

Figure 5.3 illustrates the result of different reproductive cost test-

- Figure 5.3(A): the number of Male and Female ARTs evolved in different reproductive cost is shown. Male fixed ARTs evolved in 2 to 3 times in 25 experiments with all food densities. Male conditional ARTs gradually decreased as reproductive cost was increased. Female ARTs also varied with reproductive cost. Female ARTs evolved when reproductive cost was low (1 or 2 times in 25 simulations) but no female ARTs evolved when the reproductive cost was 25 energy units or more.

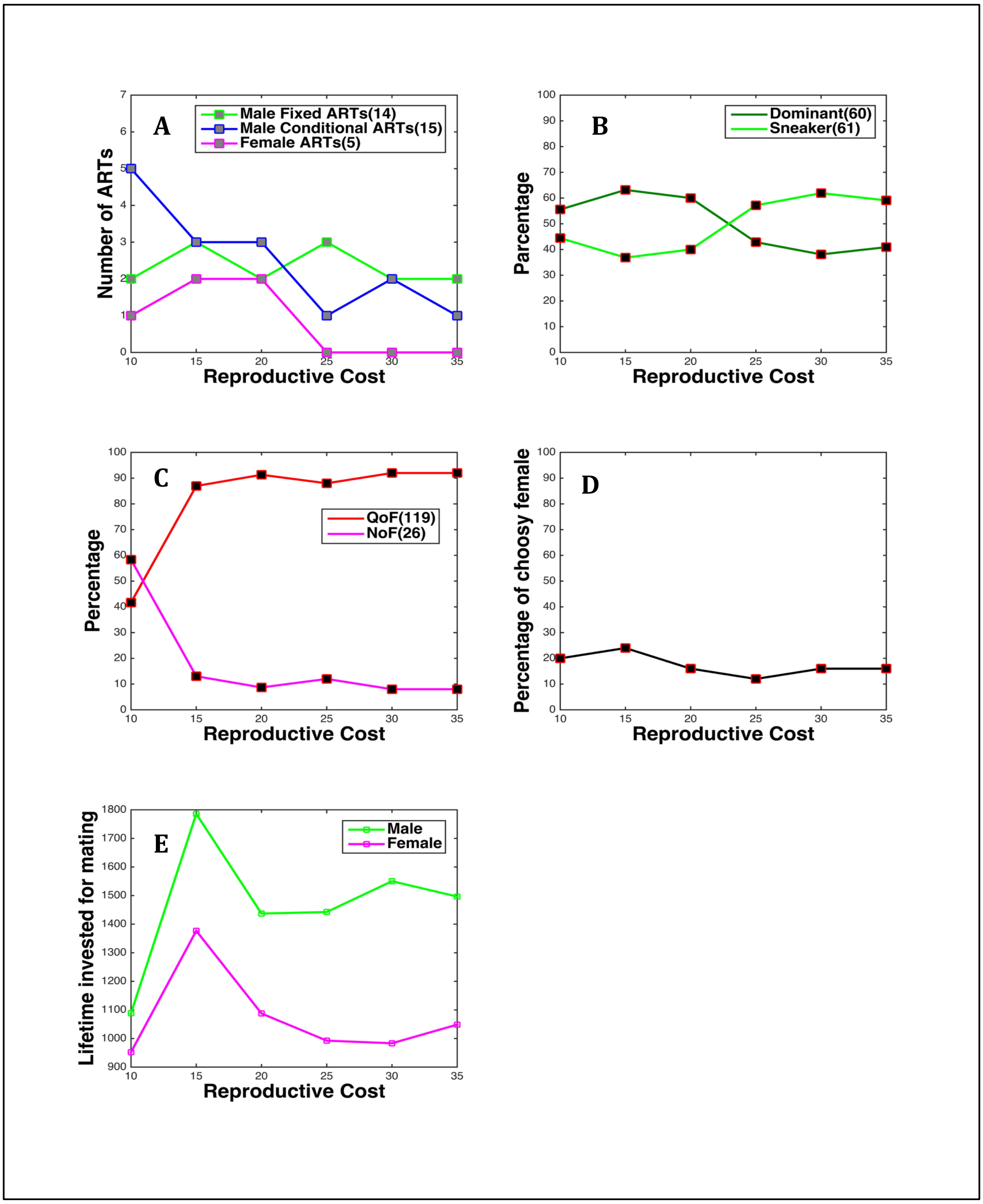

Figure 5.3 Effect of Reproductive cost on Male and Female ARTs. (A) Number of Male fixed ARTs (fixed (14) and conditional (15)) and Female ARTs (5) emerged. (B) Percentage of Dominant and Sneaker males in the populations (121 out of 150) where male ARTs not emerged. (C) Percentage of QoF and NoF female in populations (145 out of 150) where female ARTs not emerged. (D) Percentage of populations with choosy female emerged out of 150 population. (E) Lifetime investment for mating (LIM) of male and female.

- Figure 5.3(B): The percentage of dominant and sneaker males when male ARTs did not emerge (evolved populations of 121) in different reproductive cost environment. For reproductive cost up to 20, percentage of dominant males share the majority, but when reproductive cost is over 20, the sneaker males take the majority.
- Figure 5.3(C): The percentage of QoF and NoF females in the environments where
- Female ARTs did not emerge (evolved populations of 145). The proportion of QoF females was lower with the lowest reproductive cost 10, but it stayed at about 90% for higher reproductive cost.
- Figure 5.3(D): The percentage of evolved population consisting choosy female. The percentage of choosy female vary around 20% for all reproductive cost, which illustrates that, the intensity of sexual selection (female's tendency to choose male according to their quality) is about same in all reproductive cost.
- 5.3(E): Average LIM for males and females in different reproductive cost environment in the final 10 generations. Males' and Females' LIM was highest at reproductive cost 15 and gradually decreased for reproductive costs.

Male ARTs

With the increase in the reproductive cost, as the female choice regarding male quality is about same (Figure 5.3D), the number of fixed male ARTs evolved also about same (Figure 5.3A). With low reproductive cost up to 20, the LIM of female is higher and the difference between male and female LIM is relatively low (Figure 5.3E), which leads to lower competition in males for accessing female. The lower competition facilitates the emergence of conditional ARTs rather than fixed ARTs (extreme dominant and sneaker). From this reproductive cost test, it become also prominent that, conditional ARTs are more sensitive to competition level.

The percentage of dominant and sneaker males with low and high reproductive costs (Figure 5.3A) also suggests that, as female become more quality oriented and less choosy, and take lower LIM, sneaker males' percentage increases, who invest their lifetime mainly following female and either mate with female when female choose to mate or exploit female mating whenever female initiate mating with another male.

Female ARTs

The simulation with different reproductive cost reveals interesting aspects of male and female behavior, especially for females. Although the reproductive cost increases, percentage of choosy females (Figure 5.3 D) do not differ much. Therefore, the intensity of sexual selection is also about similar in all reproductive cost. But with the increasing reproductive cost, the percentage of QoF became quite higher (Figure 5.3C), as females invest more time for foraging (gain high size and energy) to produce high quality offsprings and mate few times (Figure 5.3E). Therefore, when the reproductive cost increases, rather than choosing high quality partner, females concentrate on improving own condition (size and energy) to increase offspring quality. Also, when the reproductive cost increases (up to 25 energy unit), (Figure 5.3A), as females are mainly interested to produce high quality offsprings , about 90% of the evolved populations contains QoFs (Figure 5.3C). As a result, Female ARTs disappear with high reproductive cost.

5.3 Male female Ratio

Competition between males increases when the number of males compete to access a female increases. To understand how competition between males affects the emergence of male and female ARTs, I took 6 different levels of male-female ratio by varying the number of males (60, 65, 70, 75, 80, 85) in total 100 agents in the environment with fixed reproductive cost (8 energy unit) and food density (100 food). For each competition level, I performed 25 simulation experiments where male ARTs were found for 34 times (23 fixed ARTs, 11 conditional ARTs) and female ARTs for 4 times in the evolved generation in the total 150 simulations experiments.

Figure 5.4 illustrates the result of different competition level test-

- Figure 5.4(A): the number of Male and Female ARTs evolved in different food density is shown. Male fixed ARTs evolved 3 times with lowest competition level and gradually increased to 6 times when competition level was increased. Male conditional ARTs decrease with competition level increase. Female ARTs also decreased with increased competition level.

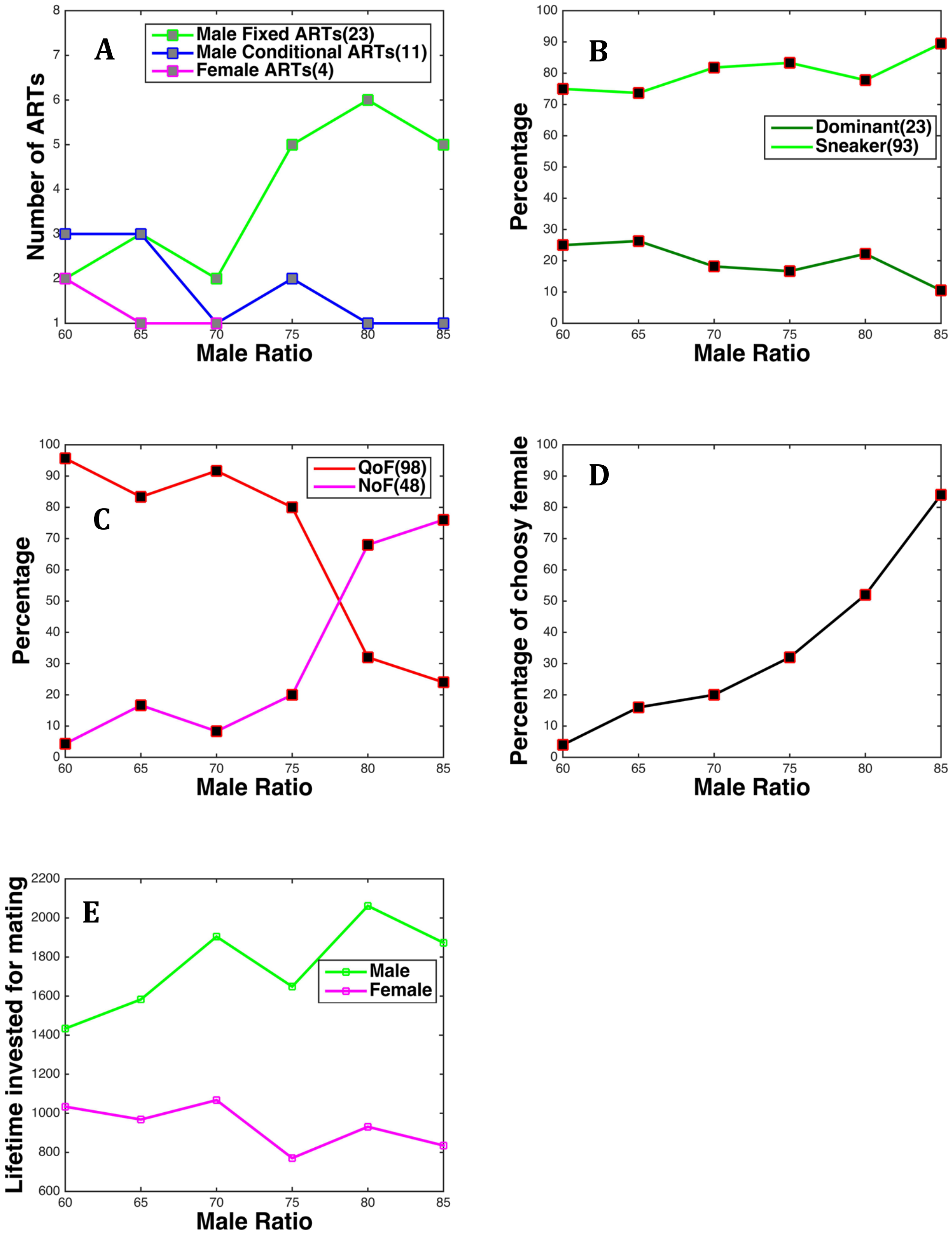

Figure 5.4 Effect of Male-Female ratio (Competition Level) on Male and Female ARTs. (A)Number of populations where Male fixed ARTs (fixed (23) and conditional (11)) and Female ARTs (4) emerged. (B) Percentage of Dominant and Sneaker males in the populations (116 out of 150) where male ARTs not emerge. (C) Percentage of QoF and NoF female in populations (146 out of 150) where female ARTs not emerge. (D) percentage of population with choosy female emerged out of 150 population. (E) Lifetime investment for mating (LIM) of male and female.

- Figure 5.4(B): The percentage of Dominant and sneaker males when male ARTs don't emerge (evolved populations of 116) in different competition level environment is shown. The percentage of sneaker males was always higher than that of dominant males.
- Figure 5.4(C): The percentage of QoF and NoF females in the environments (evolved populations of 146) where Female ARTs not emerged are shown. The percentage of QoF's gradually decreased and NoF's are gradually increased with the increased competition level.
- Figure 5.4(D): Percentage of choosy female increases significantly from 5% to 90% when male ratio (competition level) increases. That means when competition level increase, populations with choosy females (who choice male according to quality) increase significantly. Therefore, the intensity of sexual selection also increases.
- Figure 5.4(E): Average lifetime invested by male and female for mating in different male competition level environment is analyzed by taking the final 10 generations of 25 repetitions for each competition level and then averaging the results. Although Male lifetime investment for mating (LIM) increased with increased competition level, female LIM slightly decreased.

Male ARTs

As the sexual selection (percentage of choosy female) gets higher with increased male ratio, females can have strong selection of male quality (Figure 5.4D). Also with increasing male ratio, males' competition for accessing females increases. Therefore, the evolution of male fixed ARTs increased in higher rate (Figure 5.3A) when male competition level increases. Conditional ARTs gradually decrease as competition increases and females become choosy to high quality males. The females' LIM is also reduced with increased male density (Figure 5.4E), which leads to increase in the percentage of sneaker males in the environment where male ARTs don't emerge (Figure 5.4B).

Female ARTs

When the competition level is increased, with higher proportion of males, females can observe more males frequently and percentage of choosy female also increases (Figure 5.4D) significantly (80%), that is the intensity of sexual selection in very high. Rather than investing on themselves to increase offspring quality, females increase offspring number

(Figure 5.4C) and increase offspring fitness by being choosy to male quality. As a result, the percentage of NoF increases (Figure 5.4C) very high (90%) and percentage of QoF decreases very low (10%), when competition level (male ratio) increases.

5.4 Comparison of the frequency of the evolved male and female ARTs

The evolution of different number or total number of male and female ARTs depends on the environmental condition chosen for each evolution experiments. For each parameter (Food density, Reproductive cost, Male ratio), there are 6 level taken. Therefore there are total 18 parameter settings. To compare the frequency of the emergence of male and female ARTs, we did two-sided Chi-square test [112] for the 25 experiments of each parameter settings and found that, for 11 settings out of 18 settings Male ARTs are significantly more frequent (with p value<0.05) than female ARTs shown in Table 5.1

Table 5.1 Statistical (Chi-square) test to compare the frequency of the emergence of male and female ARTs. It is found that Male ARTs (red marked) are significantly more frequent than female ARTs.

Food Density	**P Value**	**Number Of male ARTs (out of 25)**	**Number Of female ARTs (out of 25)**
20	0.7471	7	6
50	0.7328	6	5
80	0.0399	8	2
100	0.0240	10	3
150	0.0047	9	1
200	0.0047	9	1
Reproductive Cost	**P Value**	**Number Of male ARTs (out of 25)**	**Number Of female ARTs (out of 25)**
10	0.0206	7	1
15	0.1228	6	2
20	0.2214	5	2
25	0.0371	4	0
30	0.0371	4	0
35	0.0740	3	0
Male Ratio	**P Value**	**Number Of male ARTs (out of 25)**	**Number Of female ARTs (out of 25)**
60	0.2214	5	2
65	0.0416	6	1
70	0.2971	3	1
75	0.0043	7	0
80	0.0043	7	0
90	0.0090	6	0

5.5 Discussion

5.5.1 Main Findings

Here I summarize how different environmental conditions affect male and female ARTs.

- Male fixed ARTs are strongly affected by female choosiness (percentage of choosy female), that is the intensity of sexual selection, and weakly by the competition level. With decreasing sexual selection intensity and competition level, male fixed ARTs also decrease (Figure 5.4A).
- Male conditional ARTs are strongly affected by the competition level and weakly by the intensity of sexual selection by females (Figure 5.2 A, Figure 5.4A). Male conditional ARTs increase with competition level decrease.
- Female ARTs are strongly affected by food density (Figure 5.2A) and very weakly by reproductive cost (Figure 5.3A). When food density is increased, female ARTs decrease. When reproductive cost is very high, female ARTs become very low or disappear.

5.5.2 Future Work

Investigate variation of multiple environmental conditions: Although we have analyzed male and female ARTs in different environmental conditions, for testing each environmental condition (food density, reproductive cost, competition level) we fixed parameter for other conditions. In future we will test and analyze the variation of two or three condition at a time such as- food density by reproductive cost, reproductive cost by competition level etc. to get more broader view of environmental condition effect.

Investigate the effect of environmental condition when male and female ARTs emerged in same environment: Male and female ARTs can emerge together in nature, although it is very rare. Also, as female ARTs are quite difficult and time consuming to find by observation or field works, there might be more female ARTs emerge with male ARTs in nature which are still undefined. In our 450 simulation environments, there were few environments where we also found male and female ARTs evolved together. In the future we plan to analyze how different environmental conditions affects the evolution of simultaneous male and female ARTs.

This chapter provides important insights about how in different environmental conditions male and female ARTs evolve in a system incorporating both natural selection and sexual selection, which are quite significant information for further investigation of the emergence of ARTs found in nature.

Chapter 6

Analysis of the ESS of Male and Female ARTs

ARTs observed in nature can be maintained by frequency dependent, density dependent or status dependent selection. Although there is a good amount of research done to find evolutionary stable states (ESS) in male ARTs [3,16], analysis of evolutionary stability for female ARTs are quite rare. In the previous chapters, I described the male and female ARTs evolved and their emergence in different environmental conditions. In this chapter, I analyze if the ARTs evolved in males and females are evolutionary stable and how the stability is maintained.

6.1 Male ARTs

To investigate the ESS of the evolved male fixed ARTs, I ran additional experiments in which the proportions of dominant and sneaker males were varied in 10% to 90%. The individuals' genotypes were taken randomly from the last 30 generations (670th-700th) of the highest fitness population with male fixed ARTs under the condition of 100 foods, 8 energy unit reproductive cost and male density 50. The experiments were repeated 50 times for each proportion of dominant and sneaker males. **Figure 6.1** shows the average fitness of dominant and sneaker males (average number of offspring) as a function of dominant male proportion. It shows that their fitness curves cross at 36% dominant male and 64% sneaker male proportion, where they are evolutionary stable. Both dominant and sneaker males have negative frequency dependent selection, that is, when the proportion of dominant or sneaker male increases, its relative fitness reduces.

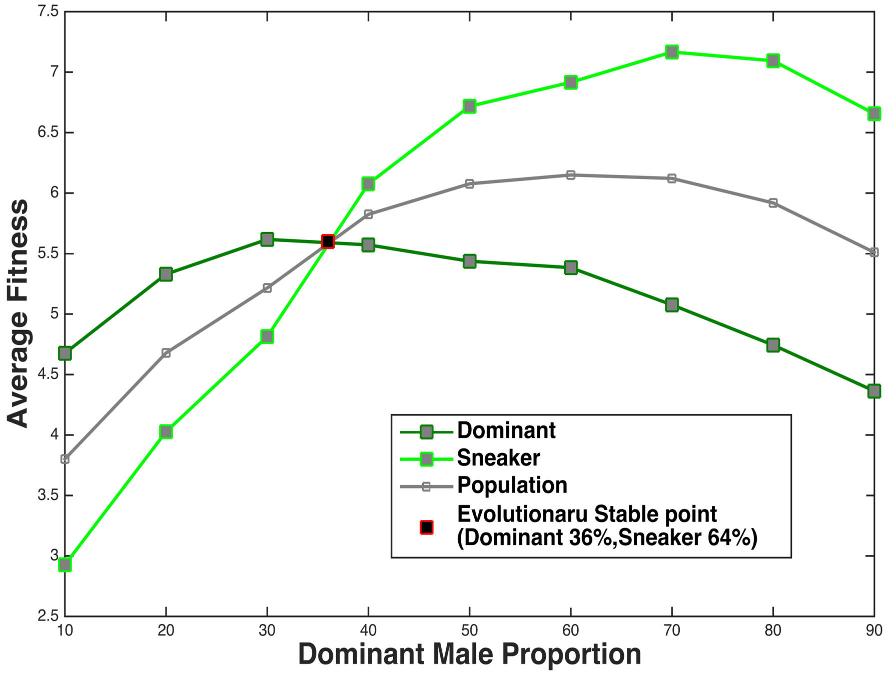

Figure 6.1 Evolutionary Stability (ESS) of Male fixed ARTs. Dominant and Sneaker males have negative frequency dependent selection and evolutionary stable at the dominant male ratio 36% and sneaker male ratio 64%.

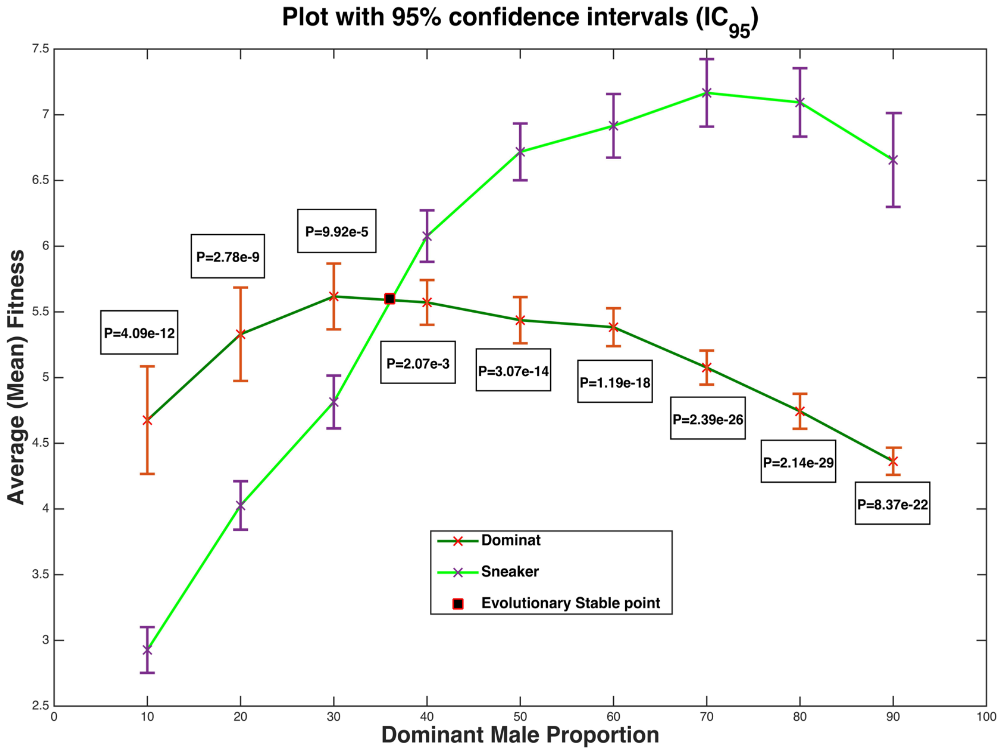

Figure 6.2 T-test analysis of dominant and sneaker males' average (mean) fitness with 95% confidence interval. The result shows that dominant and sneaker males' average fitness is significantly different with p value<0.0001.

To ensure that the mean fitness of dominant and sneaker males are significantly different except at the evolutionary stable point, I did statistical t-test on each percentage pair of dominant and sneaker male mean fitness data and found that they were significantly different with P value<0.001 (Figure 6.2).

6.2 Female ARTs

Next, I investigated ESS for female ARTs in experiments similar to that of males in which the proportions of QoFs and NoFs were varied from 10% to 90%. The individuals' genotypes were taken randomly from the last 30 generations (670th-700th) of the highest fitness population (with condition 100 foods, 8 energy unit reproductive cost and male density 50). The experiments were repeated 50 times for each proportion of QoFs and NoFs. **Figure 6.3** shows the average (mean) fitness of QoF and NoF (average number of offspring) as a function of QoF proportion. It shows that their fitness curves cross at 65% QoF and 35% NoF proportion, where they are evolutionary stable. Also it shows that, QoFs have positive frequency dependent selection and NoFs have negative frequency dependent selection. That means, when the proportion of QoF increases, it's fitness increases and when the proportion of NoF increases, it's fitness decreases.

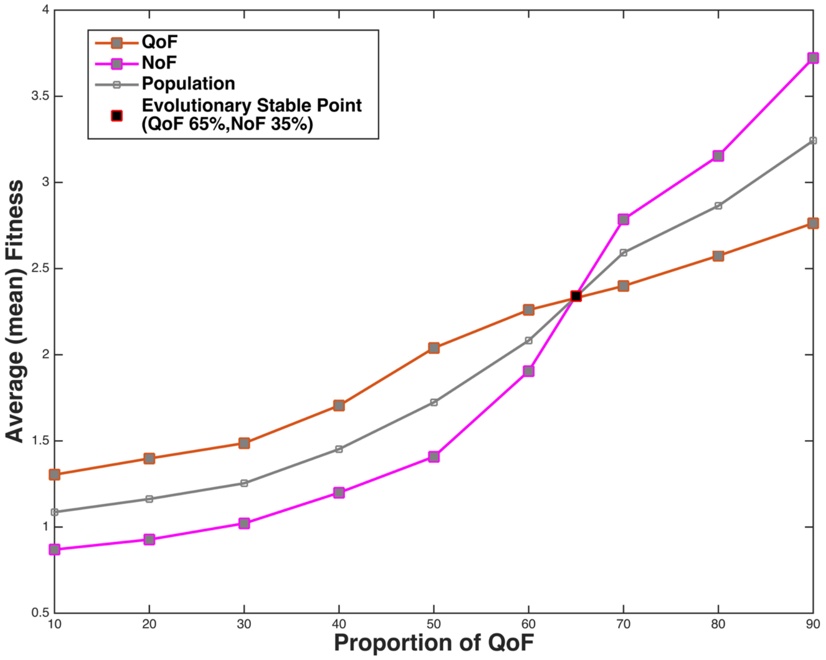

Figure 6.3 Evolutionary Stability (ESS) of Female ARTs. QoFs have positive frequency dependent selection and NoFs have negative frequency dependent selection. They are evolutionary stable at the QoF ratio 65% and NoF ratio 35%.

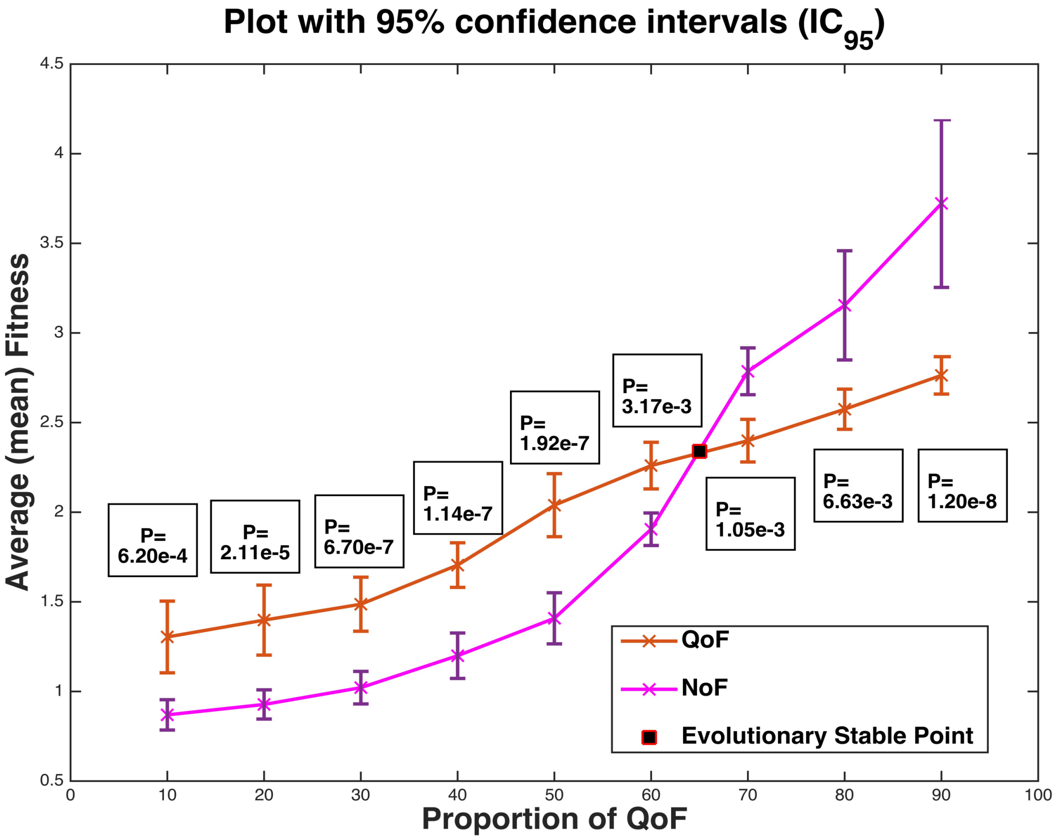

Figure 6.4 T-test analysis of QoFs' and NoFs' average (mean) fitness with 95% confidence interval. The result shows that QoFs' and NoFs' average fitness is significantly different with p value<0.0001.

To ensure that the mean fitness of QoFs and NoFs are significantly different except evolutionary stable point, statistical T-test is performed on each percentage pair of QoFs and NoFs mean fitness data and found that they are significantly different with P value<0.001 (Figure 6.4).

As in nature density dependent ESS is seen in female ARTs, I have investigated if density dependent ESS can be found in the evolved female ARTs. I ran additional experiments with the equal proportion of QoFs and NoFs in the population and changed the population size from 100 to 500 with the male-female ratio 50:50. The individuals' genotypes were taken randomly from the last 30 generations (670th-700th) of the highest fitness population with female ARTs under the condition of 100 foods, 8 energy unit reproductive cost, male density 50, and population size 100. The experiment was repeated 50 times for each population density. **Figure 6.5** shows the average fitness of QoFs and NoFs as a function of population density. In low population density, when average fitness was greater than 1 (population was growing), NoFs had higher fitness. In high population density, when average fitness was close to or lower than 1 (population was crashing), the QoFs had higher fitness. The average fitness of QoF and NoFs crossed at population density 370, near the population crash point (total population average fitness drops to 1).

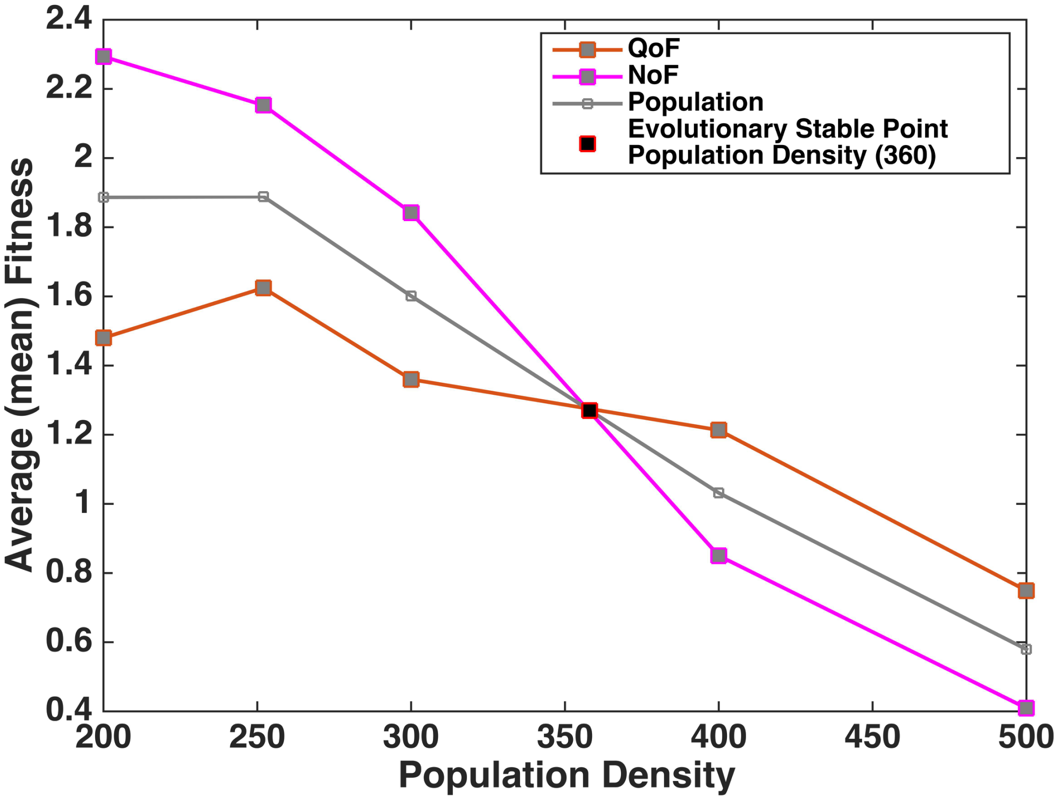

Figure 6.5 Evolutionary Stability (ESS) of Female ARTs. QoF and NoF females have density dependent selection and evolutionary stable at the population density 360, when QoF and NoF ratio is same (50:50).

To ensure if the mean fitness of QoFs and sNoFs are significantly different except evolutionary stable point, statistical T-test is performed on QoFs and NoFs mean fitness data of each population density and it is found that they are significantly different with P value<0.001 (Figure 6.6).

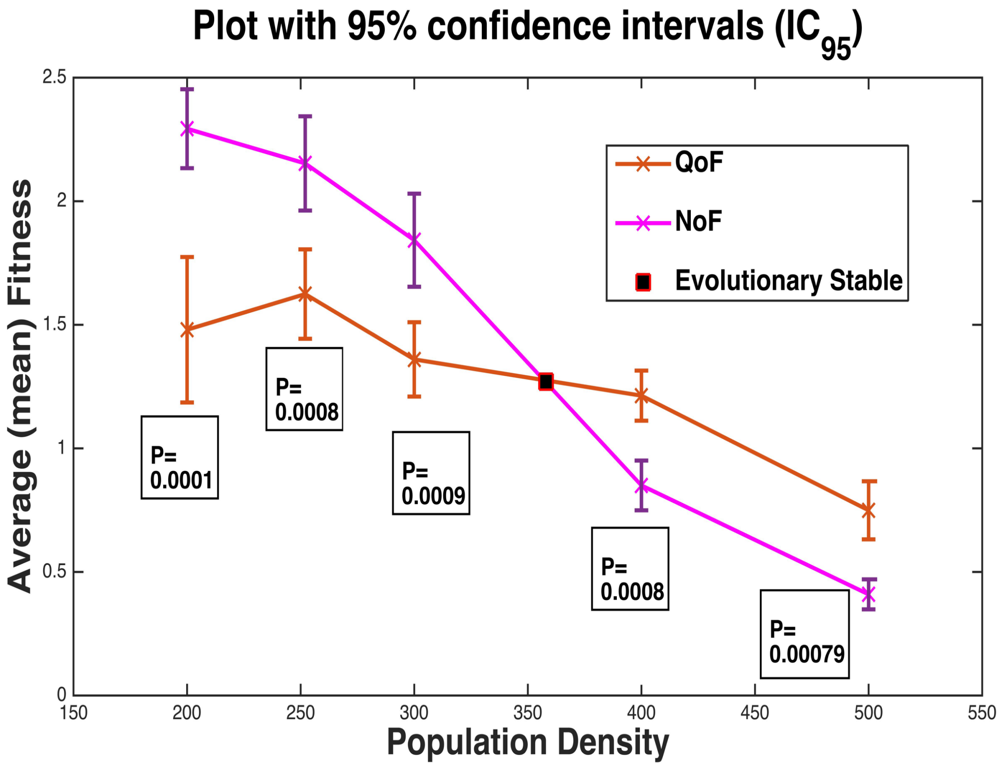

Figure 6.6 T-test analysis of QoFs' and NoFs' average (mean) fitness with 95% confidence interval. The result shows that QoFs' and NoFs' average fitness is significantly different with p value<0.001.

6.3 Discussion

6.3.1 Main Findings

Males always compete with each other to get access to female and evolved male ARTs are alternative ways to access female. The ESS of male fixed ARTs shows there is negative frequency dependent selection found in male genetically distinct alternative phenotype (dominant and sneaker). When dominant males increase, the competition between dominant males for accessing females becomes more intense, while sneaking opportunity for sneaker males increase and their fitness increases. When sneaker males increase, they have to face more competition with sneakers males. In the meantime, dominant males can increase their fitness and as there are few dominant male, female choose them more. Therefore the negative frequency dependent selection is maintained. Negative frequency dependent selection in male ARTs are also quite common in many species and investigated by many researchers [2,4,16] through different models and field works [4,24].

Female ARTs are evolved to increase either offspring number or offspring quality. It is found that female ARTs also maintain frequency dependent selection. QoFs have positive frequency dependent selection and NoFs have negative frequency dependent selection. That means, when the proportion of QoF increases, it's fitness increases and when the proportion of NoF increases, it's fitness decreases. Along with Frequency dependent selection, female ARTs also maintain density dependent selection. When population density is low, NoFs has high fitness as they produce more offspring, which leads to increase the population density. When population density turns to its higher limit, the population start crashing and the QOFs has high fitness as high quality offspring leads to greater offspring survival at high density. Although investigation of female ESS is complex, this kind of ESS is observed in females of some species. One of the best examples is females of side-blotched lizard, studied by Sinervo et al [13]. Orange throated female-produce high quantity offspring and yellow-throated female-produce high quality offspring (which are quite similar to NoF and QoF emerged in our simulation). In a seven years field experiment, Sinervo et al. [110] confirmed that there is density dependent ESS maintained in females.

6.3.2 Future Work

Investigate ESS in Male conditional and mixed ARTs: Conditional ARTs observed in nature usually have status dependent selection or evolutionary switch point. As in the experiments, I found conditional ARTs and a very few (2) mixed ARTs, my next step would be analyzing their ESS.

Investigate evolution of Male and Female ESS in different environmental conditions: Male and female ESS can be quite different and affected differently by different environmental conditions (food density, reproductive cost, competition level etc). Revealing their mechanisms could add a great value in the study of ART. I will investigate how male and female ARTs' ESS evolve with different environmental conditions.

Investigate ESS when Male and Female ARTs evolve simultaneously: Male and female ARTs can emerge simultaneously [24,110], but it is quite rare phenomenon. In our simulation, we also found few population (4 times in 450 simulation) where male and female ARTs evolve simultaneously. It will be very interesting future work to analyze how male and female ESSs emerge simultaneously in different environmental condition.

In this chapter, I ran additional simulation experiments with the evolved male and female fixed ARTs and analyzed how the ESS of male and female fixed ARTs are maintained. It is observed that male ARTs evolved due to negative frequency dependent ESS and female ARTs are due to density dependent ESS. Further analysis of ESS in different environmental conditions can also provide major understanding in the study of ARTs.

Chapter 7

Discussion

7.1 Summary of Main Findings

In this thesis, I have developed an embodied evolution framework incorporating ecological features, such as body size and energy maintenance, where male and female robotic agents interact with each other for survival and reproduction, to investigate how ARTs evolve. Unlike existing abstract mathematical [60-68] and agent based models [70-72], the agents naturally faced both intersexual and intrasexual interactions and ARTs evolved from initially continuous characteristics, which are also quite similar to the ARTs commonly found in nature [3,9,16]. This framework has higher situatedness [43] with environment than agent-based models [70-72] with robotic agents having finite body size and local sensors with limited information and moving in a space with finite dimensions and limited resources. By having a real body size and mass, larger agents can easily push away smaller agents from potential mate and win competition to access mates. Smaller agents can move faster than larger agents and quickly approach towards other agents as their velocity of the agents also depends on their size and mass. These influenced dominant and sneaker behavior to evolve in the system. Also, the sensors located on particular part of the body with limited range open up opportunities for a variety of tactics, such as sneaking from the back of an agent. Moreover, as the environment has limited energy resource and the agents' energy expenditure depends on its body size, it is possible to test how population density affects the frequency of different tactics. Overall, the evolution of ARTs is affected by the physical properties of the environment. Therefore, This kind of natural situation of evolution of ARTs from initially continuous characteristics was possible due to the embodiment with environment where we can practically see the agents evolved with different tactics and it also open the way to evolve unknown ARTs in the system, which can be further investigated in natural systems. Without embodied approach it was only possible to model genetic architecture and coexistence [40,41] of ARTs assuming that two or three distinct phenotypes were already present in male or female.

To our best knowledge, there are only two studies of ARTs where ARTs were evolved from initially continuous characteristics, done by Leif and Taborsky [42] and Elfwing et al. [59]. Leif and Taborsky studied the emergence of ARTs in a male only population in an agent-based model, which had lower situatedness than the present robotic model. Elfwing et al. evolved ARTs in hermaphrodite robots, which had high situatedness but did not include biological aspects such as size, mortality, reproductive cost. Both of the studies lacked intersexual interaction, that is, all individuals of the environment had the same sexual functionality. Therefore, this study is the first to show the emergence of ARTs in both male and female from initially continuous characteristics in a simulated embodied evolution framework, where agents face both intersexual and intrasexual interactions.

After analyzing the evolved male and female ARTs, it is found that male ARTs evolved for different tactics for accessing females, whereas female ARTs evolved for different tactics of investment in offspring. We consider three environmental conditions: food density, reproductive cost to affect female sexual selection, and male-female ratio to affect male competition level. For each condition, 150 populations are evolved to investigate how different environmental conditions affect male and female ARTs. It was revealed that-

- Male fixed ARTs are strongly affected by the intensity of female sexual selection and weakly by male competition level.
- Male conditional ARTs are strongly affected by the competition level and weakly by the intensity of females' sexual selection.
- Female ARTs are strongly affected by food density and weakly by the reproduction cost.

The intensity of sexual selection is estimated from females' mate choice, while male competition level is controlled by male female ratio in the environment. The males' quality (body size), which affects reproductive success, is visible to females and it is possible to analyze how females' response towards males depend on males' quality by analyzing the network weights of the agents. If a female chooses mating behavior for higher quality (larger size) males, we define it as choosy. In the populations where fixed male ARTs evolved, females evolved to be choosy. In the populations where conditional males evolved, females did not evolve to be choosy. That suggests that the emergence of male ARTs depends on how female behavior emerged. Alonzo et al investigated in several studies [64-66] how female choice affects the variation of different male tactics and mentioned the necessity of constructing a system where male and female ARTs can evolve together from initially continuous population. The embodied evolution model presented in this thesis fills that gap and it is found that for different male ARTs female choice also evolved differently.

Several biological and theoretical investigations [3,4,16] revealed that emergence of male conditional ARTs mainly depends on indeterminate growth and low energy cost coefficient (β) for maintaining size (section 3.1.2, (*iv*)). In this embodied evolution model, we found that, although the energy cost coefficient (β) is fixed, emergence of conditional ARTs was affected by female lifetime spent for mating (LSM), or competition level in males. When females LSM reduces compared to male LSM, males' competition to access females increase, which benefits the males staying dominant (maintaining big size with high cost to win competition accessing female) or sneaker (maintain small size with low cost and sneak) rather than being conditional.

Emergence of females ARTs are found strongly sensitive to food density and evolved females' behavior is also affected by male interaction. When female has low reproductive cost and meet with males more frequently, they can increase fitness by mating high number of high quality males. But, when females' reproductive cost gets higher and they meet with males more frequently, rather than choosing high quality male they tend to develop own reproductive condition (size and energy) and increase fitness by producing high quality offspring. Although female ARTs are observed in nature [20,21], they are not common and not well studied like male ARTs, as investigating female investment in offspring and reproduction in biological scenario is time consuming and requires complex procedures [23]. This embodied evolution model introduced an original approach in which it is quite feasible to study male and female ARTs together in the same system and to readily analyze their genotypes, morphological and behavioral phenotypes, and lifetime histories.

The simulation environments are fully stochastic and all positions (food and agents) are initialized randomly at each generation. In total 450 simulations were done by varying three environmental conditions (food density, reproductive cost, male-female ratio) and ARTs evolved in total 141 simulations. Male ARTs emerged in total 114 simulations and female ARTs evolved in total 27 simulations. Female ARTs emerged much less frequently (section 5.4 tested statistical significance) than male ARTs. The potential reason can be understood from Chapter 5 (Figure 5.2, Figure 5.3, Figure 5.4) where how the environmental condition affects the emergence of ARTs was investigated. Female ARTs were mainly sensitive to food density and evolved in higher numbers when food density was less than 80 (Figure 5.2). There were only 50 simulations done with food density less than 80, where female ARTs emerged about twice than male fixed, conditional or mixed ARTs. In the rest of 400 environments, food density was greater than 80. As a result, the number of evolved female ARTs was much lower. Environments with higher sexual selection evolved more male fixed ARTs (Figure 5.4) and environments with low competition level evolved more male conditional ARTs (Figure 5.3). Therefore, it is revealed in Chapter 5 that the numbers and types of male and female ARTs evolved depended on the environmental condition the agents are facing during simulation. Moreover, from the fitness curves (Figure 4.12), it is seen that the populations where ARTs evolve had higher fitness (chapter 5, section 5.4) than the populations where ARTs did not evolve. In these environments, evolving to behave with different tactics was more beneficial for agents than converging to similar behavior.

Investigating ESS in biological scenario could be significantly complex process [24,110]. But we can test ESS of male and feasibly manipulation proportion of phenotype, population density each. Here we have also investigated the ESS of male and female and found that male fixed ARTs (dominant-sneaker) are maintained by negative frequency dependent selection and female ARTs are maintained by both frequency dependent and density dependent selection. Male negative frequency dependent ESS and female density dependent ESS is also found in nature [8,16,24,110]. Although Male ESS is studied in large aspects [8,16], practical experiment of female ESS in very rare [24]. One special study was done by Sinervo et al [110] for female size bloched lizard and there they also found density dependent ESS in female.

7.2 Challenges and Limitations

Incorporate decentralized, open-ended embodied evolution: In this embodied evolution model, male and female interact physically and select mating partner for producing offspring in the next generation, and the next generation population is initiated without explicit fitness comparison just by random sampling from male and female offspring. To make the evolution process fully decentralized and biologically plausible, the offspring should also be placed after birth in same population with parents and let them evolve together. Moreover, by including offspring in the same population with parents, it is possible to introduce open ended evolution in the model, that can provide important insight to study biological system.

Introduce more biologically plausible genetic algorithm: The genes of the agents in this model is haploid and the genetic algorithm applied in this system is not same as biological scenario where diploid male and female genes produce offspring through gene exchange. Although this kind of genetic algorithm is presently applied to study biological system [77-84], the model will be more realistic if it is possible to apply more biologically plausible genetic algorithm.

Investigate cross over and mutation rate: Each agent had 50 genes and the crossover and mutation rate was 0.001. Therefore in 700 generations of population size 100, there were only about 70 times offspring born with a mixture of parents' genomes. Although the rate is low, meaningful ARTs evolved in the system, which is consistent with realistic scenario found in nature. But investigating the model with higher crossover and mutation rate can provide more interesting solution and evolve more unique ARTs in the system

Constraints to test the results in physical robots: In this embodied evolution model, agents are simulated robots. But there is a difficulty in testing the results with physical robots, as they have some constraints, such as they don't grow. However, it should be possible to test final evolution result by compromising some aspects, such as fixing body size of the agents according to evolved end size.

7.3 Future Directions

Incorporate male mate choice: In the simulation environment, we considered the general situation in which ARTs are found [3,4], where male quality is visible to female and female can measure male quality (input x_7, section 3.2). However, in some species, female quality is also visible to male and it is still a puzzle to understand how it affects male mate choice and emergence of ARTs in male and female [64]. As this framework is quite flexible to include new properties for evolution, it can give promising insight by including female body size in the control network input and testing how male and female

ARTs evolve in different environmental conditions. Comparing the result with current result may introduce novel aspects in the study of ARTs.

Analyze female behavior where male conditional ARTs emerge: When male conditional ARTs evolve female evolve to relax their choice on male size. Although females don't choose males according to quality (size), females can easily chase away or avoid small males when they are not interested in mating. Also, relatively larger males can move away smaller males to access female. However, to understand male female interaction in conditional case, doing further investigation will be interesting to reveal more clear aspect of their behavior. It is possible to do create and test different scenario along with input of male female agents where conditional ARTs emerge.

Incorporate determinate growth: In the simulation environment, we considered indeterminate growth as ARTs are more commonly found with animals having indeterminate growth [3,4,16]. As the model is quite flexible, in future we can also test simulation with agents with determinate growth and compare the results of emerged ARTs.

Investigate combination of environmental conditions: We evolved the male and female in three environmental conditions (food density, reproductive cost and male-female ratio). To get broader aspect of the environmental condition, it will be interesting to evolve and investigate ARTs (male and female) in combination of environmental conditions (such as food density× reproductive cost, reproductive cost × male-female ratio).

Investigate when both Male and Female ARTs evolve simultaneously: Male and female ATRs can emerge simultaneously [24,110], but it is quite rare phenomenon. In our simulation, we found few populations (4 in 450 simulations) where male and female ARTs evolved simultaneously. It will be very interesting future work to analyze how male and female ARTs evolve and interact simultaneously in different environmental conditions.

Investigate ESS of conditional ARTs: Although we investigated ESS for genetically distinct ARTs, conditional ARTs also has ESS called evolutionary switch point. It will be interesting to investigate ESS of conditional ARTs along with the affect of environmental condition in male and female ESS.

Extend the model to investigate other reproductive systems: Along with dioecious (male and female) animal, hermaphrodites (can play both male and female function) also evolve alternative reproductive behavior by allocating sexual function differently to increase reproductive fitness, mostly depending on their physical (age, size) conditions and environmental conditions [3,4]. Moreover, more complex androdioecious (males and hermaphrodites) and gynodioecious (females and hermaphrodites) systems are also found in nature where individuals evolve to play different sexual functions (male, female or hermaphrodite). In a broad sense this scenario is closely related with alternative reproductive behavior, as individuals evolved to play different sexual functions as alternative reproductive behavior [4]. This embodied evolution framework is flexible enough to further analyze species of different sexual mechanisms (hermaphrodite, androdioecious, gynodioecious, etc.).

Extend the model to study social and multi-agent role allocation: Moreover, in addition to biological studies, this study can help build ideas about role emergence in multi-agent systems and social systems. Here the emerged alternative reproductive tactics are evolved as optimal role for a system. So, this line of research can also give deeper insight about understanding how social role emerges from group interaction or what optimal roles would be appropriate in some multi-agent systems, where multiple groups interact and negotiate to complete a task in an optimal way.

Test the results in physical robots: In this embodied evolution framework, agents were simulated robots and all the experiments were done in simulated robot environments. We had also planned to test the result in real smartphone robots (Figure 3.1). The robots can be 3D printed or painted in different colors to be recognized as male or female. Another way is to show the color blob in smartphone screen to show its gender. Robots can transfer genotype by blue tooth communication, or when they are in a short distance, they can show their genome interpreted as QR code to other robot. As real robots do not grow, our plan is to test the final generation result with their evolved end body size. It is possible to add parts to the smartphone robot base for changing its body size. Even though we do not currently have 100 mobile robots available, the most convenient way is to use embodied evolution method of Stefan Elfwing [94], where he successfully did embodied evolution experiments with a population of 80 virtual agents using 4 physical Cyber Rodent robots. Unlike simulation environment, testing with real robots provides actual physical environment including occlusion, real physical interaction along with more realistic input information in the neural network controller, which can potentially give us more interesting and realistic results such as hiding behind other agent for sneaking, courting female by blocking another potential partner from female’s sight etc.

Chapter 8

Conclusion

In this thesis, I developed an embodied evolution framework with simulated robotic agents incorporating ecological features, such as body size and energy maintenance, where male and female robotic agents naturally face both intersexual and intrasexual interactions for survival and reproduction. To clarify the important properties for understanding full picture of ARTs, first I performed an overview of alternative reproductive tactics (ARTs) and exiting models of ARTs in terms of situatedness, that is embodiment with the environment. Then I constructed the original embodied evolution framework including the properties (emergence from initially continuous characteristics, intersexual and intrasexual interaction, high situatedness with environment). In simulation experiments, different forms of male and female ARTs evolved and I clarified distinct morphological and behavioral phenotypes and genotypes associated with those ARTs. The effects of environmental conditions (food density, reproductive cost, male-female ratio) on the emergence of male and female ARTs were investigated which reveals that- male fixed ARTs are sensitive to sexual selection, male conditional ARTs are sensitive to competition level and female ARTs are sensitive to food density. Finally, ESS of male and female ARTs was analyzed to show that male ESS is negatively frequency dependent and female ESS is both frequency and density dependent. This study of ARTs through this embodied evolution framework does not only contribute in the field of ARTs with novel aspects but can also be used as an important tool to understand the concept of role emergence in multi-agent systems or social behavior.

Parts of this work has been published in "Artificial Life and Robotics" conference [111], where all the model development, simulation and analyses are done by FARZANA RAHMAN.

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