WHAT WILL WE LEARN?
A MATHEMATICAL TREATISE OF CULTURAL EVOLUTION

Pontus Strimling

2008

School of Education, Culture and Communication
WHAT WILL WE LEARN?
A MATHEMATICAL TREATISE OF CULTURAL EVOLUTION

Pontus Strimling

Akademisk avhandling

som för avläggande av Filosofie doktorsexamen i Matematik/tillämpad matematik
vid Akademin för utbildning, kultur och kommunikation kommer att offentligen
försvars tisdagen, 25:e mars, 2008, 13.00 i Lambda, Mälardalens högskola, Västerås.

Fakultetsopponent: Professor Robert Boyd, UCLA, USA.
Abstract

In this thesis we apply mathematics and formal modeling to study culture from an evolutionary standpoint. Cultural evolution theory is based on the belief that we can increase our understanding of human behavior by studying how culture is created and spread. Together with my co-authors I use mathematical modeling to investigate why we need a theory for cultural evolution, what it can tell us, and how we can test such a theory.

The thesis consists of an introduction and five papers. The first paper is an empirical test of whether we need to know the history of a population to be able to determine what culture they will have. The second paper looks at the circumstances under which a genetic predisposition for imitating parents could evolve. The third paper looks at the accumulation of neutral traits, that is, cultural variants that flow between people at random without affecting their fitness; neutrality provides an important null hypothesis to other explanations of why we have the culture that we do. The fourth paper makes an attempt at defining what makes a cultural variant successful, and thereby reveals some important differences between genetic and cultural evolution. Finally, the fifth paper investigates a model that can be used to study mechanisms of cultural evolution in laboratory experiments.

ISSN 1651-4238

Abstract

In this thesis we apply mathematics and formal modeling to study culture from an evolutionary standpoint. Cultural evolution theory is based on the belief that we can increase our understanding of human behavior by studying how culture is created and spread. Together with my co-authors I use mathematical modeling to investigate why we need a theory for cultural evolution, what it can tell us, and how we can test such a theory.

The thesis consists of an introduction and five papers. The first paper is an empirical test of whether we need to know the history of a population to be able to determine what culture they will have. The second paper looks at the circumstances under which a genetic predisposition for imitating parents could evolve. The third paper looks at the accumulation of neutral traits, that is, cultural variants that flow between people at random without affecting their fitness; neutrality provides an important null hypothesis to other explanations of why we have the culture that we do. The fourth paper makes an attempt at defining what makes a cultural variant successful, and thereby reveals some important differences between genetic and cultural evolution. Finally, the fifth paper investigates a model that can be used to study mechanisms of cultural evolution in laboratory experiments.

Keywords: cultural evolution, mathematical modeling, game theory.
Sammanfattning


I den sista artikeln i avhandlingen undersöker jag tillsammans med min handledare Kimmo Eriksson en ny modell för att testa idéer sprids i ett datorlabbe vilket skulle låta oss använda samma metoder som redan visat sig mycket användbara i ekonomi och psykologi.


Nyckelord: kulturell evolution, matematisk modellering, spelteori.
Preface

This thesis is the result of five years of exploration. When I started the project I knew two things: firstly, that doing mathematics was fun. Secondly, that the idea of being able to use math to understand everyday behavior was exiting. This idea was presented to me by Kimmo Eriksson. Before that I only really thought of doing pure math, especially as I had little knowledge of the natural sciences where mathematics is usually applied.

I hardly knew anything about mathematical modeling of human behavior when I started, and what is more unusual is that neither did my supervisor. Kimmo had done plenty of mathematical research but the idea of applying mathematics to social science was one he just recently thought of. For me this was the perfect situation, I got to explore freely with someone as excited as me by my side. We went through stacks of books, discussed for hours and formulated some interesting models in the process.

Among the books we read was *Culture and the Evolutionary Process* by Rob Boyd and Peter Richerson [22]. This book stood out from the others in that it was really building up a theory bit by bit. This seemed like the right way of doing models; not just as isolated descriptions of phenomena but as parts of a grander map of human behavior.

I read up on the authors and found that Pete Richerson was treasurer for the Human Behavior and Evolution society and that they where hosting a conference that summer in Germany. With nothing to lose I went to Berlin and found myself in a strange world filled with 2D:4D research, debates about the modularity of the human mind and Pete, who actually ended up inviting me to do research with him in UC Davis. This was a very important year for me as I believe that it is crucial that someone who wants to model human behavior with mathematics has a good understanding of both mathematics and of the processes he or she tries to model. While Kimmo knew everything I needed and more on the mathematical side, UC Davis and the people there gave me a new understanding of the issues at hand.

So here we are and the thesis you are now reading is the result of many people taking an interest in teaching me the things I needed to become a modeler of human behavior. I want to take this opportunity to thank some of the people who got me here. First and foremost Kimmo Eriksson who have been more than a supervisor to me. He has been an advisor, a co-worker and a friend. Simply put, a true mentor. I also want to thank Pete Richerson. Without his invitation to Davis and his hospitality while I was there this thesis would not be as good. I would like to thank
Ken Binmore for taking the time to answering all my questions and showing me what game theory and research can be if you add true vision to the research process. I would also like to thank Magnus Enquist who became my co-supervisor when I got back from Davis. He has taught me how important it is to really understand the answer as well as the question posed. These senior researchers has given me the kind of gifts that can never be repayed. I can only hope to be able to give as much to future students as they have given me.

I would also like to take the opportunity to thank my co-authors of which there have been many. Perhaps most prominent among the ones not already mentioned are Richard McElreath who took me under his wing in Davis and Jonas Sjöstrand, who has given me a glimpse of how mathematics can be done.

Finally I would like to thank friends and family for supporting me. I hope all of the people who helped me will enjoy this presentation of mathematical modeling of cultural evolution.
The following papers are included in this thesis:

**Paper I** P. Strimling, Culture cannot be determined by genes and natural environment alone: An empirical study of online game behavior.

**Paper II** R. McElreath, P. Strimling, When natural selection favors imitation of parents.

**Paper III** P. Strimling, M. Enquist, K. Eriksson, Which traits will win in Cultural Evolution?

**Paper IV** P. Strimling, J. Sjöstrand, M. Enquist, K. Eriksson, Neutral cultural evolution

**Paper V** P. Strimling, K. Eriksson, Explore and Collect; a Framework for testing Cultural Evolution
Contents

Preface iii

I Mathematical models for social science in general and cultural evolution in particular. 1

1 Introduction 3

Introduction 3

1.1 Mathematical models for human behavior 3
1.2 Mathematical methods 6
  Game Theory 6
  Optimal stopping. 7
1.3 Cultural Evolution Theory 8
  The history of the spread of Cultural Evolution Theory 9
1.4 Important questions in Cultural Evolution. 11

Bibliography 15

II Papers 17
Part I

Mathematical models for social science in general and cultural evolution in particular.
Chapter 1

Introduction

During the last five years I have learnt so many things: every co-author, every book and every paper I have read has taught me something. And then there are all the discussions that I have had with friends and family, with people who agreed or disagreed with me. I have learnt so much from so many sources that I can’t remember it all, I don’t remember all the things they taught me or all the tools they showed me. Even among the tools I remember I only use a few and among the theories I have heard I only agree with some.

So which things do I remember? Which tools am I using? Which ideas am I defending and which do I remember but disagree with? And all the people who taught me things, where did they learn them? Why did they remember them? These questions may seem mundane but I believe that understanding why certain ideas spread and why others don’t is at the heart of understanding human behavior. I also believe that mathematical modeling is the key to understanding these issues, and these two beliefs build up the central theme of this thesis.

The thesis is based on 5 articles about cultural evolution. The purpose of this introductory chapter is to outline the greater story of which these papers are parts. Specifically the contents are as follows. Section 2 is about mathematical models, presenting arguments for why they are important. Section 3 describes the particular methods used in this thesis. Section 4 gives a short introduction to mathematical modeling of cultural evolution theory and an overview of its history. Finally, in Section 5 I present what I believe to be the important questions that a theory of cultural evolution must answer and I discuss how the papers presented here tie into them.

1.1 Mathematical models for human behavior

There can be no doubt that mathematical models have made a huge contribution to the natural sciences. This thesis grows from the belief that mathematical modeling can be equally beneficial in the social sciences; indeed, that the great questions
1. Introduction

about human behavior can not be solved without rigorous modeling and that right
now there is no language more appropriate for these models than mathematics. In
this introduction I will try to argue in favor of this belief.

In this thesis a particular area of mathematical modeling called Cultural Evo-
lution is investigated and expanded. Before presenting what Cultural Evolution is
and why it is important I will discuss the more general question of the usefulness
of mathematical modeling in the social sciences.

Webster defines social science as "a branch of science that deals with the institu-
tions and functioning of human society and with the interpersonal relationships of
individuals as members of society". Although some mathematical modeling is done
in almost every sub-field within social science it seldom has the central position that
it has in natural science. What can mathematical modeling do for social science?
What is its role? This is an important question that in itself falls under the realm
of social science but outside the scope of this thesis. That being said I will in this
introduction discuss it briefly and give my personal opinions in the matter.

When studying any phenomenon the question posed and the answer given can
be categorized into one of three categories: describe, explain or predict. So how
can mathematical modeling help in understanding the phenomena studied by so-
cial science? When it comes to describing, statistical descriptions are based on
implicit mathematical modeling. Here there are plenty of statistics already being
used and even more models that are not very broadly used but that could easily
be implemented. My feeling is that when it comes to statistics, social science is
better served by increasing the awareness of the models that already exist than by
developing new models. Clear and precise descriptions of the world, on the other
hand, give useful insights into what is needed for a mathematical model to capture
the essence of a phenomenon, so it is very important that modelers make use of the
rich descriptive social science that already exists.

When it comes to explanations there can be plenty of insight gained from for-
mulating the explanation in a mathematical model. It helps in making sure that
the logic is correct, and in bringing assumptions into the light to be scrutinized in
their own right. Finally a model can give insight into how a specific explanation
can be tested empirically.

This brings us to the prediction category, perhaps where general formal models
are most useful. Given that the model captures the important parts of reality it
will almost by necessity give predictions that can be tested.

I believe that predictions should be at the heart of social science. Understanding
what happens when certain reforms are made, how groups of people act when hit
by disaster and what is needed to change culture are predictions that, if properly
answered, would bring great benefit to society. In fact, one could argue that social
science predictions are among the most important public services that can be given
in a democracy as they are the prerequisites for educated voting. For instance, when
voting on the Euro, voting for or against the Euro in and of itself is uninteresting.
Instead we vote on what happens if the Euro is introduced versus if it is not. We
vote on social science predictions and the more correct these predictions are, the
more educated decisions we make.

So what are the benefits and drawbacks of a mathematical modeling? First of all any model is an extreme simplification of reality. This is both its greatest flaw and its most positive feature. The only full model of reality is reality, and when we can understand reality directly we do not need models. But since almost every question is too complex to be understood directly there is a need for simplifications. Mathematical models have the benefit of being very explicit about the assumptions made. The reader gets insight into what has been assumed about reality so that he/she can either agree with it or attack it directly. The fact that so many simplifications need to be made is what makes it necessary for the modeler to have a good understanding of the nature of the problem, because otherwise the things that are at the heart of the problem might be assumed away. Later on I will discuss how the history of formal Cultural Evolution theory has been affected by the fact that both mathematical modeling skills and an understanding of the phenomenon under study are needed for a researcher to be able to contribute to the field.

Formal models can be divided into three levels: general argument, analytical solutions and simulations. A general argument is a statement that is true given a small set of assumptions, so small that the specifics of a particular model are not included. This makes the result true for a wide variety of models and therefore it stands on firmer ground. For instance, in paper 3 we make a general argument concerning the effects that vertical transmission have on what kind of traits spread in cultural evolution. Often these arguments seem almost tautological when realized.

An analytical solution is the end result of an analytically solved model. Compared to the general argument the results here are specific to the model. On the other hand they are usually expressed so that it is clear how the variables affect each other. Most of the papers in this thesis deal with analytical solutions.

Finally, simulations are results that only hold for the simulated values. Even though modern computer power makes it possible to simulate even complicated models for a wide array of values there are always limitations. For instance, in paper 4 we use simulations to see the difference between a new model that is analytically solvable and the old model that is not, and we find that there is little difference between the two. This is a good example of how a problem that may seem unsolvable by analytical methods can be solved with only small and reasonable changes to the model.

When faced with a problem too complex for general arguments or analytical solutions there are two choices: either you simulate or you make further simplifications. Even though I understand that in some cases further simplifications are impossible without taking away essential parts of the model, I argue that as far as possible one should use analytical solutions rather than simulations, and general arguments rather than analytical solutions even at the risk of oversimplifying. One reason for this is the greater generality of the conclusions as mentioned above, another is because the more general the result, the easier it is for other researchers to build on it. A general argument can be taken at face value and put into any system that uses the same assumptions. An analytical solution makes it possible to add
1. Introduction

things to a model and see how it changes the results. This building block property is, I believe, extremely important for the field in which the modeler is acting, even if it isn’t important to show the result that he/she is trying to show at the moment.

If an analytical solution can be found for at least a simplified version of the problem one can always use simulations to show that the results seem to hold even for a more complex version of the model.

1.2 Mathematical methods

There are many methods existing in math that can be used in social sciences and many new ones can be invented if needed. In this thesis I use game theory, both evolutionary and standard, and in paper 5 I use optimal stopping. Here follows a brief introduction to these methods.

Game Theory

Game theory deals with strategic decisions. In general, a model (called a game) is made, and a solution is derived from that model. The underlying hypothesis is that real people who are sufficiently used to playing the “game” in question will tend to act such that they maximize their own utility. A solution to a game is called an equilibrium, and the one generally used is the Nash equilibrium. This means that all the players play so that no one can benefit (raise their utility) by unilaterally changing strategy.

Game theory as a discipline was established in 1944 by John von Neumann and Oskar Morgenstern in their book Theory of Games and Economic Behavior [21]. In this book they aimed to show that “the typical problem of economic behavior becomes strictly identical with the mathematical notions of suitable games of strategy”, implying that economic behavior can be modeled by the use of mathematics. Their notions are very much in line with the ones that I outlined above.

Von Neumann and Morgenstern knew that they were starting a new field of science and in their book they discussed the stages that such a science would undergo. It would start with small problems with almost self-evident solutions and then build up more complicated situations which would give answers beyond the obvious, and in the end reach “the field of real success: genuine prediction by theory”.

For decades, game theory was mainly concerned with solving internal problems. Solution sets were defined, games of different types were developed and solved. As the basic notions of game theory were developed, the theory started to be useful for the social sciences. Economist Colin Camerer [5] observes that “in the past fifty years, game theory has gradually become a standard language in economics and is increasingly used in the social sciences”.

6
Experimental Game Theory

Although game experiments have been carried out for fifty years, they really got started in the 1980’s. By then it had been widely recognized that people often did not act in accordance with all of the standard theories. For example the advanced equilibrium selection theories that had been proposed almost all fell flat [5].

The contribution of experiments is that people’s actual behavior can be recorded in a controlled environment. The importance of experimental testing of theories can not be stressed enough; it was simple experiments that overturned Aristotelian thinking in physics and simple experiments that gave insight into patterns of genetic inheritance. In the same way, game theory has generated beliefs about human behavior that was wrong and simple experiments now conducted have overthrown these premature beliefs and led to a vitalization of the entire discipline of game theory with several controversies still unresolved.

The experiments presented in paper 5 are made with the techniques that have become standard within experimental game theory. Our results indicate that a popular explanation of why people deviate from optimal behavior in a optimal stopping problem (see below) seems to be incorrect.

Evolutionary game theory

John Maynard Smith adopted and expanded the concepts of game theory to better fit the common assumptions in biology. Among the more important changes here was to exclude rationality in favor of a dynamic system where any strategy that does well propagates. Maynard Smith also introduced the concept of an Evolutionary stable state, which is a Nash equilibrium with the added condition that a small amount of mutants, if introduced, are still worse off than the current population. The early work in this field is well summed up in Evolution and the Theory of Games [18]; for a more current summary I recommend Evolutionary Game Theory [25].

Optimal stopping.

The secretary problem

As an introduction to the field of optimal stopping I will give you the perhaps best-known problem of the field, the secretary problem. In this problem, Bob wants to hire a secretary and has several applicants to go through. For some reason he can’t have callbacks but must hire someone on the spot. Bob wants to hire the best secretary. The question he wants answered is how to choose in order to maximize the chance of hiring the best of the applicants. As each applicant is being interviewed, Bob must either hire the applicant (and end the decision problem) or reject the applicant and interview the next one. To make this decision Bob knows only how many he has evaluated and their relative rank.

The first step in solving this problem is realizing that the solution takes the form of a threshold rule; the optimal tactic is to look through a certain percentage
of all the applicants, then use the best level observed as a threshold and finally choose the first one that’s better than the threshold.

Why must the optimal tactic look like this? Well, it is never worth choosing an applicant who is lower than one already looked at, as this can not be the best applicant. The only question remaining is whether or not to accept an applicant who is the best of all yet observed, and the only parameter on which we can base this decision is how many applicants we have gone through. The argument can be made more mathematically explicit, see Fergusson [14].

The next step in solving the problem is to make the chance of finding the best applicant, given a certain breakoff point, explicit. Define \( n \) to be the number of applicants, \( r \) to be the number of applicants before breaking off, and \( P(x) \) to be the chance of \( x \) happening.

\[
P(\text{Finding the best applicant given breakoff point } r) = P(\text{The best is not among the first } r \text{ and the best is reached}) = P(\text{The best is not among the first } r) \cdot \sum_{i=r+1}^{n} P(i \text{ is the best}) \text{ and } P(i \text{ is reached } | i \text{ is the best}) = \frac{n-r}{n} \cdot \sum_{i=r+1}^{n} \frac{1}{n-r} \cdot \frac{r}{i-1}
\]

Now when we have made this explicit all that is left is to maximize it. As \( n \) grows large, \( \sum_{i=r+1}^{n} \approx \int_{r}^{n} dt \). Doing this substitution turns maximizing the explicit expression into a simple exercise, and we find the answer to be \( r \approx 0.37n \). So the optimal rule is to look through 37% of the applicants before making any hiring decision.

**Optimal stopping in general**

Optimal stopping theory is of course more than the secretary problem, and in a broader view it can be presented as dealing with when it is the best time to act in a certain way based on sequential random events. It has mainly been used in operations research, where the action taken may be when to reorder stock or when to replace a machine, and in statistics where the action may be to test a hypothesis or to estimate a parameter.

For a good mathematical introduction to this field I refer to Fergusson [14]. In this thesis, optimal stopping is used in paper 5, in the context of people exploring among many possible options each giving different rewards. The optimal stopping question here is when to stop exploring and use the best one already explored.

### 1.3 Cultural Evolution Theory

When trying to understand the full range of human behavior it soon becomes obvious that understanding genetic evolution is far from enough if you want to be able to describe, predict and explain the wide array of phenomena that human behavior contains. Cultural evolution is the study of how ideas are born, spread and die.
Cultural Evolution Theory

This is often combined with genetic evolution to form dual-inheritance models but, as we will see can stand on its own as well.

Like all theoretical approaches this one has its advantages and its disadvantages. The main focus here will be: What phenomena are studied with cultural evolution theory? What does it try to explain, describe or predict? And how well does it do it?

First of all, let’s define culture. Richerson and Boyd define it like this: 

Culture is information capable of affecting individuals’ behavior that they acquire from other members of their species through teaching, imitation and other forms of social transmission. [22]

The three major trends in Cultural Evolution theory (CE) can be summed up with the three questions:

- Why is there culture?
- How did culture affect the human biology?
- What culture will spread under what conditions?

The answer to the first question focuses on the genetical predisposition humans have for culture and try to explain how they evolved, i.e. CE theorists study what benefit culture had to early humanoids.

The answers to the second question are generally derived by using models of dual inheritance, that is, models where the agents inherit genes from some source and culture potentially from some other source. Using these models CE investigates how culture should have affected the evolution of our genome. As a classical example, Feldman and Cavalli-Sforza use co-evolutionary models to study the spread of lactose tolerance [13]. A more recent example is the idea that culture has promoted the evolution of genetically based altruism in humans. This idea is commonly named strong reciprocity theory and has caused much debate ([2] and [22]). The second paper in this thesis assumes that there is a genetic predisposition in whether or not we should imitate our parents, and then goes on to look at when a dual-inheritance system will promote parent imitation.

Finally the third question concerns what culture will spread under what conditions. Generally the models for this has focused on the conditions under which traits that enhance genetic fitness will spread. But recently there have been several papers looking at the accumulation of culture [11] i.e. how much culture will amass under different circumstances. In paper 3 we look at the evolution of traits that differ in other ways than whether or not they are fitness enhancing, and in paper 4 of this thesis we look at the accumulation of neutral traits.

The history of the spread of Cultural Evolution Theory

The idea that one can gain insight about human behavior by treating culture in an evolutionary perspective is old. Indeed, Darwin mentions it in The Descent of Man.
1. Introduction

[8]. Here, however, we focus on mathematical models for cultural evolution, which has a much shorter history.

As I have discussed above, to make mathematical models for cultural evolution one needs a mathematical understanding as well as knowledge about how culture spreads. As there is no field that trains its students in both of these things, there are not so many people who have the necessary requirements. The field of anthropology for example, which is generally concerned with the spread of ideas, usually give no training in mathematics for its students. However, you do not need a good understanding of mathematics to realize the potential of evolutionary models. So when we look at the history of modeling CE we see that while the people in the field generally get a decent amount of positive recognition, there are not many others who pick up their ideas and advance them.

Theoretical biologists with an interest in behavior and evolutionary modeling are perhaps the people with the best training to address CE and we will see that many of the people who have done substantial work in the field have this background\textsuperscript{1}. Likewise many of the important papers of the field have been published in theoretical biology journals.

In 1965, Donald Campbell published a paper by the name of "Variation and Selective Retention in Socio-Cultural Evolution" in which he launched the idea of modeling cultural evolution formally [6]. Campbell received some positive feedback on the paper and among other things he got to hold the address at the American Psychological Association in 1975. Within 10 years from Campbells' address at American Psychological Association three books had been written filled with mathematical models of cultural evolution. All of them were written by pairs of people combining mathematical knowledge with the right social science knowledge base. The three books were *Genes, Mind, and Culture: The Coevolutionary Process* by Charles Lumsden and Edward O Wilson [16], *Cultural Transmission and Evolution* by Luigi Cavalli-Sforza and Marc Feldman [7], and finally *Culture and the Evolutionary Process* by Rob Boyd and Peter Richerson [22]. They present similar but distinct arguments about how cultural evolution should be modeled.

*Genes, Mind, and Culture* has a macroscopic perspective, where questions about the accumulation of cultural traits are raised. It received some heavy criticism, mainly on the basis that the mathematical models were ill connected to the verbal arguments in the book. In particular this point was raised by John Maynard Smith and Neil Warren in their book review [19]. Due, perhaps, to this criticism this is the least cited of the three books.

*Cultural Transmission and Evolution* portrays culture as a type of phenotypical extension of our genetical predispositions for acquiring it. The perspective here is very much a microscopic one. *Culture and the Evolutionary Process* also used microscopic models but tried to focus more on making the theory accessible for social scientists. This might have worked in its favor as it is by far the most cited

\textsuperscript{1}Peter Richerson, Marc Feldman, E.O Wilson and my own supervisor Magnus Enquist all have this background
of the three books. Both of these books received mainly positive criticism, but on the whole remarkably few researchers have expanded on this work.

Two exceptions are Alan Rogers and Kevin Laland. In 1988, Alan Rogers published the influential paper *Does Biology Constrain Culture?* [23] in which he shows that contrary to the assumptions generally held, culture could arise and spread without increasing the average fitness of the population. Apart from leading to a response from Boyd and Richerson [4], Rogers’ paper affected how models were made. The paper still receives direct responses [10].

Kevin Laland came from psychology and started to work with Feldman in 1992. This brought another field into the mix, making cultural evolution studies even more cross-disciplinary.

In the mid-nineties both Boyd and Richerson had started to train Ph.D students to acquire all the necessary skills for the cross-disciplinary work. New collaborations started with economists such as Samuel Bowles and Herbert Gintis. These economists brought with them experience in simulation that since has been more common in the field.

In the last few years, several independent lab groups have been created that devote themselves to CE models. Worth mentioning are Kevin Laland’s group at the University of St Andrews, Michel Raymond’s group at Montpellier University and the group in Stockholm of which I have been a part the last two years.

So right now there is a rapid increase of research on Cultural Evolution. This is probably a result of the fact that more people with the appropriate background are entering the field.

1.4 **Important questions in Cultural Evolution.**

In this section I will present five questions that I believe are central to CE. Some of them have been addressed but on most of them there has been no research until recently. Each of the questions introduces the core in one of the five papers in the thesis and I will present the papers as I discuss the questions.

**Is cultural evolution theory useful?** I have earlier discussed what questions CE tries to answer. There have, however, been very few empirical tests made to see whether or not the models give correct predictions. In *Not by Genes Alone* [22] Boyd and Richerson try to convince the reader that culture matters. They argue that it is not enough to look at genes, natural environment and the interplay between them to predict behavior, you need to look at the cultural history as well. This is a difficult claim to test since it is hard to find two identical environments. However it is an important claim to test. Before we see if CE is correct about the way culture spreads we need to see if culture has enough of an impact on human behavior for CE to be important.

In the first paper of this thesis: *Culture cannot be determined by genes and natural environment alone: An empirical study of online game behavior*, I
look at social contracts in the game World of Warcraft™. World of Warcraft is played by millions of people on identical but separate servers. This gives us separate populations with roughly the same genes and identical natural environments. The cultural trait that I have chosen to study is how people divide rewards that they have gotten through collaboration. I find that there is very little difference in behavior within the servers but very large differences between servers. This suggests that history has a substantial part in forming peoples culture.

**Who do we imitate?** This question is at the core of CE and the answer to it gives us an understanding of who are the most successful spreaders of culture. This in turn gives us insight into which culture will spread and at what speed. For instance, should we expect people to have a conformity bias or not? A conformity bias means that agents tend to imitate the majority more than what would be expected if they imitated at random. E.g. if a cultural trait is carried by 75% of the population conformity biased individuals will have more than a 75% chance of acquiring that trait. Early work in the field argued in favor of the adaptive value of conformist bias [3]. This notion has recently been challenged by another theoretical paper [12]. Without going into the details of the arguments it is safe to say that this debate could be settled by empirical work. The argument is about whether or not there is an adaptive value of a trait, and while this is interesting in and of itself it can’t show whether or not the bias exists. Only empirical work can show this.

In a similar way I have, together with Richard McElreath, looked into an issue that recently stirred up debate in psychology. With the book *The Nurture Assumption*, Judith Harris [15] questioned the implicit assumption that parents are the major cultural rolemodels. Using a co-evolutionary approach we look into when it is fitness enhancing to imitate from your parents, compared to imitating a random member from the population. This is a good example of when modeling can be used to compare the strength of two effects working in different direction. On the one hand it is beneficial to imitate your parents since they have shown signs of high fitness by having at least one child (you). On the other hand, if you are a person predisposed to imitating, there is a higher probability that your parents are too and this increases the probability that the information they have is old. Our model suggests that, unless the environment is very stable, it is more beneficial not to imitate parents. This theoretical result is presented in detail in the second paper of this thesis *When natural selection favors imitation of parents.*

This is also one of the easier results to test empirically. Indeed empirical data from humans as well as birds tend to show that very little culture is imitated from parents, see [15] and [17].

**How do trait characteristics affect cultural evolution?** If we see each cultural trait as a replicator, much in the same way as it is suggested in memetics
Important questions in Cultural Evolution.

[1], they have characteristics which help or inhibit their ability to be spread. While many models look at characteristics of the system in which the traits spread, little work has been done on how the trait characteristics affect the spread. To my knowledge, the only trait characteristic that has been studied in a mathematical way is the fitness benefit the trait incurs to the individual carrying it, as we do in paper 2 of this thesis. This lack of modeling seems somewhat peculiar given that the main idea of the field of memetics is to see the world as if cultural traits rather than people were the agents [1]. However, memetics has for some reason become a field of highly abstract discussion and definition making. While this may be of some interest, I believe that it is more productive to build up models that give concrete predictions and then move on to test them empirically. When we know which types of models give correct predictions and which do not we can step back and talk about which definitions are useful and which are not.

In the third paper in this thesis, Which traits will win in Cultural Evolution? I, together with my supervisors Magnus Enquist and Kimmo Eriksson, make a first attempt at investigating the effect of trait characteristics that, while not incurring biological fitness to the individual, affect how easily the trait is acquired and deserted.

Analysis of our model points to interesting differences between cultural and genetic evolution. The differences come out of the fact that in genetic evolution a person gets all of her traits at the same time, while in cultural evolution a potential adapter of a new trait may already have some other cultural trait that can affect whether or not the new trait is adopted.

**Why is there an accumulation of culture?** It is clear that humans have accumulated an amazing number of cultural traits. In fact there are several indications that in some cultural domains like mathematics and music, this accumulation process is increasing exponentially [11]. However the focus in CE has been to look at the spread of single traits rather then the amassing of multiple traits (with the exception of [16]). In the fourth paper of this thesis I, together with my colleagues Jonas Sjöstrand, Kimmo Eriksson and Magnus Enquist, look at a neutral evolution model of the cumulation of culture.

In brief we find an analytical solution for how different variables such as population size and learning efficiency affect the amount of neutral traits in a population. Among other things we find that, in our model, for any substantial amount of culture to be upheld in the population you need a learning efficiency close to one. And we find that when the learning efficiency is close to one a little increase in it has a large impact on the amount of cultural traits in the population. This effect can be part of the explanation to why humans have so many cultural traits while most other animals have so few.
1. Introduction

How does CE fit with experimental work? How well does the CE models fit with how people actually use social learning in an experimental setting? This is another of the unanswered questions in CE. Only recently has cultural evolution been brought into the lab [20] and then with mixed results. I believe that it is crucial for the future of the theory that it is tested and that it proves it can explain behavior in controlled settings. If this doesn’t happen, it is hard to imagine that the theory will have much value in explaining the real world. In the fifth and last paper in this thesis, Explore and Collect: a Framework for Testing Cultural Evolution, I, together with Kimmo Eriksson, introduce a new model of optimal stopping that we hope will provide a more fertile ground for experimental work on cultural evolution. In brief we introduce a model where the players get to choose for how long to explore before settling for the best of the ones already picked. We argue that this model captures the main features of many everyday choices in people’s lives as well as some important choices made in the EEA. On top of this the model is analytically solvable and easily extended to incorporate several aspects of CE. We argue that this makes the model a good candidate for experimental work on cultural evolution. Finally we conducted an experiment where we tested how people handled the problem in the lab. We found that they search a little bit more than optimal but other than that show a intuitive understanding of the situation.

In conclusion, there are important problems facing cultural evolution theory, but the results in this thesis show that we need the theory and that these problems can be dealt with. I believe that the most important task ahead lies in constructing models that are easily testable either in a computer lab or preferably in reality. By testing theories and weeding out the wrong ones cultural evolution theory can become a part of a larger predictive social science theory.
Bibliography


Part II

Papers