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Experimental and theoretical models of cultural evolution

Marius Kempe

Abstract:

This thesis contributes to the field of cultural evolution by presenting two experimental and two theoretical models of cultural evolution. Prior to presenting these I survey existing experimental and theoretical models of cultural evolution. In the first experiment, I test the hypothesis that increasing group size speeds up cultural accumulation, using a novel puzzle-solving task and within a transmission chain design. I find support for this hypothesis, in contrast with previous experiments. In the second experiment, also using a transmission chain design, I examine perceptual errors in recreating Acheulean handaxes and ask whether such errors can account for the variability of Acheulean technology over time. Using the accumulated copying error model to compare the experimental data to archaeological records, I conclude that perceptual errors alone were likely not the driving force behind Acheulean evolution. In the first theoretical chapter, I present models of cultural differences between populations and of cumulative culture, which build on existing models and accord with empirical data. I then show that the models, when combined, have two qualitative regimes which may correspond to human and nonhuman culture. In the second theoretical chapter, I present a ‘fundamental theorem of cultural selection’, an equivalent of Fisher’s Fundamental Theorem of Natural Selection for cultural evolution. I discuss how this theorem formalizes and sheds light on cultural evolutionary theory. Finally I conclude and discuss future research directions.

Experimental and theoretical models of cultural evolution

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Declaration:

Some of the chapters of this thesis were co-authored in collaboration with other researchers. Where this is the case the other researchers are named at the beginning of the relevant chapters.

Statement of Copyright:

The copyright of this thesis rests with the author. No quotation from it should be published without the author's prior written consent and information derived from it should be acknowledged.

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Introduction

The topic of this thesis is experimental and theoretical models of cultural evolution. Cultural evolution here refers to the theory that culture – which, in this field, is defined as information transmitted via social learning, although very different definitions are and have been used in other parts of anthropology – evolves in a broadly Darwinian way: that is, by a process of variation, inheritance, and competition, which leads to selection on cultural traits (Mesoudi et al., 2004). This process leads to the phenomenon of cumulative culture, in which the utility of complexity of individual cultural traits increases over time, such as in human science and technology and such that no one individual could invent them in their lifetime (Boyd & Richerson, 1996; Tomasello, 1993). It is this capacity for cumulative cultural evolution that, arguably, has allowed our species to successfully colonize and inhabit virtually every terrestrial environment on the planet in a relatively short period of time (Richerson & Boyd, 2004; Hill et al., 2009).

The study of cultural evolution is now over three decades old. A good number of both experimental and theoretical models have been constructed and analysed, to which this thesis contributes four novel models. The aim of the thesis is to contribute to our understanding of cultural evolution, both empirical and theoretical, by using some of the specific techniques of the field, including ‘transmission chain’ experiments, mathematical models, and computer simulations. The previous results of studies using these methodologies will be surveyed in the first chapter.

The first chapter comprises a selective literature review of previous models of cultural evolution. It is divided into two parts, which survey previous work relating to two questions:

1. How are cultural traits changed during their transmission?
2. What social learning strategies do individuals use and what are the population-level consequences of those strategies?

These two questions provide a framework and launching pad to discuss developments both old and recent in the field.

Thereafter follow two experimental and two theoretical chapters. In Chapter 2, I describe an experiment seeking to understand the link between demography and cumulative culture, which has been the subject of both previous models and experiments. I present a novel experimental task in which participants solve jigsaw-puzzles, which I argue has several advantages over previous tasks. Using this task, I show that the hypothesized positive effect of the size of a cultural group on the rate of cultural accumulation can occur in an experimental situation, as predicted by previous models but contrary to previous experiments.

In Chapter 3, I describe an experiment which tests a particular mathematical model of cultural evolution in Acheulean handaxes. This technology was prevalent for over a million years in hominin evolution and had extraordinary stability in form over this time. Using a novel iPad-based experiment in which participants manipulated a virtual handaxe image with their hands, I tested the Accumulated Copying Error model, in which cultural evolution takes place solely through cultural mutation due to perceptual errors. After analyzing the model, fitting our experimental data to it, and

comparing the result with archaeological records, I conclude that cultural mutation cannot have been the only process at work in Acheulean evolution.

In Chapter 4, I construct and analyse two theoretical models: one of cultural differences and one of cumulative culture. Here ‘cultural differences’ refers to the phenomenon that multiple populations of one species show distinct ‘profiles’ of cultural traits, which, while a hallmark of human culture, has also been observed in non-human species such as chimpanzees and orangutans. I show that such distinct profiles can be maintained even in the case of repeated innovation and frequent migration. In the model of cumulative culture I show that both the number of cultural models and the accuracy of social learning affect the degree to which trait complexity increases. I note that both models fit available empirical data (on the differences in great ape populations and the degree of complexity of human Oceanic fishing technology). I then combine the models, showing that the combined model, which incorporates both cultural differences and cumulative culture, has two qualitative regimes which seem to correspond with human and nonhuman culture.

Finally, in Chapter 5 I take inspiration from R. A. Fisher’s ‘Fundamental Theorem of Natural Selection’ to construct a similar ‘fundamental theorem of cultural selection’. This theorem provides a precise mathematical expression of the process of cultural selection in a general way. I derive and explain the theorem and argue that it allows a unifying perspective on a number of cultural evolutionary forces that have been hitherto considered separately, including content, model, and frequency-dependent biases, natural selection, and cultural group selection.

Chapter 1.

Experimental and theoretical models of cultural evolution: a review

A revised version of this chapter was accepted at *WIRE Interdisciplinary Reviews: Cognitive Science*.

Abstract:

The field of cultural evolution is now over thirty years old, and a good deal of work has been done. This paper reviews models of cultural evolution, both experimental and theoretical, and surveys what they can tell us about cultural evolutionary processes. The models are grouped into two categories, according to which of two broad questions they address: (i) How are cultural traits changed during transmission?, and (ii) What social learning strategies do organisms use and what are their population-level consequences? The review is selective, not exhaustive, and attempts to survey both the most important works and recent developments.

1.1. Overview

Cultural evolution is now a field with over thirty years of history. The main principle of this field is that culture evolves in a Darwinian manner – that is, through a process of natural selection on cultural traits. Culture, in this usage, is taken to mean any information that is transmitted from individual to individual via social learning (Mesoudi et al., 2004). To be clear, the kind of natural selection that is posited to act on culture does not necessarily rely on biological fitness, but rather constitutes a separate cultural evolutionary process which may be called 'cultural selection'.

The argument for this idea is relatively straight-forward. Cultural traits, such as technological inventions, languages and linguistic features, religious and social customs, and so on, clearly vary (amongst each other), reproduce (from individual to individual), and compete (for memory or adoption). For example, there are around 6800 languages in the world, and approximately 5 million distinct patents have been issued in the US since its founding (Mesoudi et al., 2004). Languages are clearly learnt socially, while patents build on and cite earlier patents. Finally, competition takes place between cultural traits within these system, such as the replacement of many irregular verbs with regular verbs in English since medieval times (Lieberman et al., 2007) and the replacement of certain stone tools with other types in the archaeological record (O'Brien & Lyman, 2000). Thus, there is every reason to think that a process of natural selection will take place amongst them, which to distinguish it from the process of natural selection on biological organisms (i.e. through genetic reproduction) is often called cultural selection. A detailed appraisal of the evidence for this argument can be found in Mesoudi et al. (2004).

The idea that natural selection acts on culture is in fact rather old; for example, Darwin mentions it in *The Descent of Man* (1871). Since then a large number of other scholars in many fields have discussed this idea: famous examples include James (1880), Campbell (1965), Dawkins (1976), Popper (1979), Skinner (1981), Cavalli-Sforza & Feldman (1981), Boyd & Richerson (1985), Hull (1988), and Dennett (1995). The true beginning of the field, however, may be taken to be the books by Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985), which were the first to develop this idea in a thorough, quantitative way. Since then a good deal of detailed work has been done, which has recently been surveyed accessibly by Mesoudi (2011a).

The aim of this chapter is to review the more specialised literature of models, both experimental and theoretical, which has accumulated since the founding books of Cavalli-Sforza & Feldman and Boyd & Richerson. The advantage of modelling is that it can shed light on complex phenomena and produce insights by simplifying inessential features. Experiments can model situations observed in real life, while allowing controlled designs and detailed data recording. Mathematical models provide a way of running formal ‘thought-experiments’, by analyzing the consequences of a certain set of assumptions that are thought to hold in the real world, and provide a level of precision that is unattainable through purely verbal models. Thus modelling, which has greater internal validity (that is, internal consistency and logical coherence), is an important complement to observational research such as ethnographic field studies, historical and archaeological research, and statistical data mining, which have greater external validity (that is, direct relation to the phenomena being studied) .

The review will be selective, rather than exhaustive, as the literature after thirty years is extensive. The review will also focus exclusively on cultural evolution, rather than the interaction of cultural and biological evolution – itself an important and large topic with a varied literature known more specifically as gene-culture coevolution (see Durham 1991; Laland 2008). The review will also be exclusively focused on humans, excluding the large and diverse literature on social learning in non-human animals.

The review is structured around two important questions in cultural evolution:

1. How are cultural traits changed during their transmission?
2. What social learning strategies do individuals use and what are the population-level consequences of those strategies?

1.2. How are cultural traits changed during transmission?

This question encompasses two sub-questions which I will separate for the purposes of discussion. First I will discuss how cultural traits change during transmission generally, for example through the actions of remembering and perceiving. Second, I will discuss how cultural traits increase or decrease in utility during transmission, leading to the phenomenon of cumulative culture.

It is well known that traits change simply through the process of learning, or copying, on the part of a naive individual. This process was first studied experimentally by Bartlett (1932), who pioneered the 'transmission chain' method. In this method, one individual is seeded with a cultural trait of some kind – for instance, a story or a

picture – and then this individual transmits the trait in some way to a second individual, who in turn transmits the trait to a third, and so on. The method can also be varied to have more than one individual in each link of the 'chain', so that a group of individuals in some way transmit a trait to another group of individuals. Finally, in this group setting, the 'turnover' of the chain can be altered so that instead of the entire group changing at every step, only one individual is replaced in the group by a new individual; this is known as the 'replacement' method and was first proposed by Gerard et al. (1956). The bulk of experiments pertaining to cultural evolution have been conducted with the transmission chain method and its variants (Mesoudi & Whiten, 2008).

A large number of specific traits have been investigated with these methods, and different questions have been asked. The studies of Bartlett and his school (e.g. Maxwell, 1936; Northway, 1936; Ward, 1949; Hall, 1950) tended to use stories and drawings, and to frame open-ended research questions: what patterns could be found in the changes to the traits as they were passed along the chain? Secondly, they asked how characteristics of the subject – for example, their cultural background or social status – may have affected the changes seen in the traits. Specific hypotheses did not tend to be tested, and the general conclusion was that traits tended to lose detail and resemble preconceived notions of the individuals as they were transmitted. For example, in one of Bartlett's (1932) experiments, an American Indian story called the 'War of the Ghosts' was passed through a transmission chain made up of British participants, with the result that details such as the names of the warriors were lost, and unfamiliar elements such as the American Indian notion that something black

came out of a dying warrior's mouth were transformed into the more familiar Judao-Christian idea that his soul was leaving his body.

However, the focus of these studies was on human psychology – memory – and not on cultural traits and their evolution. More recent studies have reappraised this method with a view to understanding the details of cultural evolution. Thus, for example, Mesoudi et al. (2006) found that social information in stories was transmitted more accurately and lost less frequently than non-social information, in line with 'social brain' theories that posit that human cognition evolved primarily to deal with social information. Bangerter (2000) found that gender stereotypes were superimposed on descriptions of scientific phenomena, with initially neutral descriptions of conception gradually transformed such that sperm cells were increasingly attributed active agency and ova increasingly attributed passive non-agency. Many similar experiments now give us a reasonable, detailed understanding of the variation in traits caused by the process of transmission, comprehensively reviewed in Mesoudi & Whiten (2008). These variations constitute examples of what is called 'cultural mutation' by some (e.g. Cavalli-Sforza & Feldman, 1981) in the literature.

Researchers have also attempted to model these processes of change through transmission mathematically. The leading methodology here is the 'Bayesian' approach exemplified by Kalish et al. (2007), Smith (2011), and Xu et al. (2013). In this approach individuals are thought of as possessing 'prior', innate or learned, biases for certain characteristics of cultural traits (e.g. simplicity or learnability). They then observe 'data' from another individual composed of samples from a distribution of

traits with varying characteristics. The models suppose that individuals combine these two sources of information using Bayes' theorem and create a 'posterior' distribution of trait characteristics which they present in turn to the next individual. This approach has had remarkable success in producing predictions qualitatively in accord with experimental results, even in experiments not originally designed to test the models (e.g. Beppu & Griffiths, 2009, who created a Bayesian model which recreated the experimental results found by Jacobs & Campbell, 1961; their results are discussed below). Because of its focus on the details of cognition and its predictive success, it represents one of the most promising approaches for future research devoted to elucidating the details of cultural transmission.

While all of the afore-mentioned studies were carried out in a laboratory situation with a carefully controlled experimental design, an important recent development has been the use of an 'open diffusion' method by Whiten & Flynn (2010) and McGuigan & Cubillo (2013), in which the individuals with whom the new trait or information is seeded are allowed to freely interact with a social group and the transmission of the trait is observed. This technique allows researchers to document previously unobservable features of cultural transmission, such as who chooses to observe what and whom; for example, McGuigan & Cubillo (2013) found that male children were more likely to transmit gossip than female children, and that both sexes were more likely to transmit gossip than surprising factual information. The downside of this method is of course that experimental control and some precision is lost. Despite this, it represents another promising avenue of research for the future.

The second sub-question, namely how cultural traits accumulate over time, has a shorter history. Cumulative culture, as discussed above, refers to traits such as the startling technological, scientific, artistic, and social achievements of humanity, which are distinguished from the cultural traits of other animals by their reliance on earlier, less developed traits (Mesoudi et al., 2004). Experimental work on cumulative culture using the transmission chain method was initiated by Caldwell & Millen (2008). In their experiments, individuals perform a technological task with a clear goal and measure of success, such as constructing a paper airplane to fly as far as possible or building a tower using spaghetti and clay as high as possible. Each participant completes this task as best they can, after which successive individuals in the chain are faced with the same task but are able to observe the previous individual's solution. The focus in these experiments is generally less on the nature of the cognitive processes involved in the task, and more on the degree to which successive individuals are able to improve on their predecessor's solution, and the conditions which exacerbate or attenuate this improvement.

Caldwell & Millen (2008) found that the quality of solutions did improve as the designs were transmitted through a chain, indicative of cumulative cultural change. In further studies Caldwell & Millen (2009) addressed whether particular mechanisms of social learning - imitation, emulation, or teaching - are necessary for cumulative cultural change. Imitation involves copying behaviours (here, the motor actions required to make the paper airplane), emulation involves copying end-products (here, the finished airplane design), while teaching involves the transmission of explicit advice (here, advice about how to make the paper airplane). They found that, for this task, each of these three mechanisms were sufficient alone, in contrast to previous

claims that only imitation and teaching (and not emulation) are necessary for cumulative culture (Heyes 1994). Caldwell & Millen (2010), meanwhile, found that allowing individuals to observe more than one model simultaneously does not increase the rate or degree of accumulation.

This last result is intriguing because several mathematical models of cultural accumulation have focused on the relationship between population size and the rate and degree of cultural accumulation. That population size is an important factor in technological evolution in particular is suggested by both apparent links between increases in population sizes in the Upper Paleolithic and the concurrent appearance of so-called 'modern human behaviour' (including complex stone tools, decorations, cave art, and musical instruments) (Shennan 2001; Powell et al. 2009), and by the drastic loss of technologies in Tasmania after the area became an island circa 10,000 years ago and therefore was cut off from neighbouring Australia (Henrich 2004). These observations led Shennan (2001), Henrich (2004), and Powell et al. (2009) to construct models in which increases or decreases in population size led to increases or decreases in the rate and/or degree of cultural accumulation in the population. This effect occurs because in larger populations complex skills are less likely to be lost due to random transmission error, and rare beneficial modifications are more likely to be made, as there are more people to make them. More recent models have added several realistic features: Mesoudi (2011b) showed that an increasing cost of learning more, and more complicated, traits would produce realistic S-shaped curves in the degree of complexity of over time, which had not previously been found. Finally, Pradhan et al. (2012) considered the effect of varying levels of interaction between members of the population, aiming specifically to explain the greater quantity of technologies found

in chimpanzee populations compared to orangutan populations, and showed that this could be caused by the greater sociability of chimpanzees.

While chimpanzee populations may have *more* cultural traits than orangutans, neither species, nor any other nonhuman primate species, appears to exhibit *cumulative* culture. The social and cognitive factors that may be responsible for this difference have also been explored experimentally. Dean et al. (2012) had groups of capuchins, chimpanzees and children solve a three-stage puzzle box to obtain rewards, with each solution predicated on the previous one(s). The children significantly outperformed the monkeys and chimpanzees on this minimally cumulative task, with verbal communication, imitation, and prosociality predicting the greater success in children. It is likely, therefore, that both socio-cognitive (e.g. imitation fidelity) and social demographic (e.g. population size/density) underlie the species differences in cumulative culture, an issue that is addressed in Chapters 2 and 4 below.

More recently two experimental studies have revisited the hypothesis that cultural accumulation is facilitated by larger population sizes. Derex et al. (2013) found that simple (arrowheads) and complex (fishing nets) computer-designed traits were maintained only in larger groups of 8 or 16 participants, and not in smaller groups of 2 or 4 participants. Muthukrishna et al. (2014) found that complex symbol designs and difficult-to-tie knots were only maintained in transmission chains comprising five participants per generation, and not chains composed of a single participant in each chain. The negative finding of Caldwell & Millen (2010), therefore, may have been due to the particular task that they used, which may not benefit from social learning as much as the tasks employed in these subsequent studies.

1.3. What social learning strategies do individuals use and what are their population-level consequences?

Like the previous question, this question naturally divides into two subquestions: the first concerns what social learning strategies we empirically observe organisms using, and the second the theoretical population-level consequences of these strategies.

'Social learning strategies' here refers to the innate or learned rules which people use in social learning (Laland 2004): rules specifying, for instance, what or from whom to learn; an equivalent term is 'transmission biases'. The use of the term 'bias' here is intended in a statistical sense, as indicating a deviation from 'unbiased', or undirected/random social transmission (rather than the normative sense of, say, 'racial bias'). While there has been a good deal of theoretical work investigating what social learning strategies natural selection may favour (e.g. Boyd & Richerson, 1985; Kendal et al., 2009a), in the end there is clearly only one way to definitively establish what social learning strategies people use: empirical observation and experiment. Accordingly the first part of this section will focus on experimental work while the second section, dealing with the population-level consequences of given social learning strategies, will focus on mathematical models, which allow such questions to be answered with suitable generality.

Here I will focus more on strategies that concern from whom and what to copy, and less on strategies concerning when to copy (e.g. depending on life-history variables: for a review, see Kendal et al., 2009b). This focus is appropriate because 'who' and 'what' questions are more directly relevant to understanding the population-level consequences of social learning strategies, which is one of the primary aims of cultural evolutionary theory. For the same reason, cultural evolutionary research is

generally less concerned with the specific mechanism by which social learning takes place, such as imitation, emulation, teaching, social enhancement, and so on - as long as there is some mechanism to provide relatively faithful transmission, who and what is copied is more important at the population level than how it is copied - and for this reason the majority of research in social psychology (e.g. Bandura, 1977) and comparative psychology (Whiten et al. 2004) is only tangentially relevant to the intent of this review.

Social learning strategies relevant to cultural evolution can be divided into three categories using a convenient classification system due to Richerson & Boyd (2005): namely, as falling into one of three kinds of biases, either 'content', 'model', or 'frequency-dependent'. Content biases refer to strategies in which individuals choose a particular trait over others because of innate or learned preferences for the actual content of that trait, be it meaning, usefulness, or aesthetics. Model biases refer to strategies in which individuals adopt traits because of a characteristic of the person from whom they learn the trait: for example, adopting a trait from prestigious or generally successful individuals. Finally, frequency-dependent biases refer to strategies in which individuals take up a trait because of the trait's relative popularity, or unpopularity, compared to other traits in their population; examples of this include conformity, which (in cultural evolution, but not in the broader field of psychology) is defined as adopting the most popular trait in a population with a probability greater than its proportion of occurrence in the population, and anti-conformity, where the least popular trait is adopted with a probability greater than its proportion of occurrence.

While some authors have described the transmission chain studies discussed in the previous section as furnishing examples of content biases (e.g. Mesoudi, 2009), in my view content bias differs from cultural 'mutation', or from the memorability of a cultural trait by the fact that individuals choose the relevant trait in some fashion. Using this definition, there has been unfortunately little work on content biases, as in transmission chain studies participants generally do not have a choice between different cultural traits. One of the few studies is that of Wisdom et al. (2013), in which participants had to find the highest-scoring combination of 'items' in a virtual environment in which they could view other participants' items and scores. They found that content bias was an important element in participants' social learning strategies, with participants copying the highest-scoring items in addition to deploying model- and frequency-dependent biases. Further studies explicitly examining content biases in an experimental setting are clearly needed.

There have been more studies examining model biases. A number of early studies found strong effects of perceived expertise or status on people's judgements in domains such as aesthetic judgements (Mausner, 1953), visual perceptions (Mausner, 1954), gambling (Rosenbaum & Tucher, 1962), and attitudes (Ryckman et al., 1972). There has also been work specifically focused on children's learning, since a great deal of what we know is learned as children, with a number of studies finding that children preferentially copy from older rather than younger models (Brody & Stoneman, 1981; Abramovich & Grusec, 1978; Jaswal & Neely, 2006). In an innovative experiment Wood et al. (2012) recently found that children were biased more towards older models than self-professedly knowledgeable ones where these characteristics conflicted. Using adult participants, Mesoudi (2011c) conducted a

study in which participants constructed virtual (computer-based) projectile points to conduct virtual hunts (with variable rewards) and were able, during multiple rounds, to view and possibly copy other individuals' points. This experiment found evidence for the presence of success bias but noted that the presence of the bias was heterogenous: rather than all individuals using it, some individuals used it very often and others barely at all (note that this was success rather than content bias, as the participants were not aware of the utility of specific virtual projectile points). Using a similar paradigm, Atkisson et al. (2012) found that individuals were more biased towards model characteristics, specifically the prestige of a model as indexed by the amount of time that other participants were said to have looked at the model's arrowhead designs, than trait characteristics, i.e. the effectiveness of the arrowhead.

Finally, a number of studies have examined frequency-dependent biases, primarily conformism. The famous early studies of Sherif (1936) and Asch (1952), which convincingly demonstrated that people may sometimes adopt the opinions of the majority, do not qualify as conformity under the cultural-evolutionary definition because it is not possible to tell whether people adopt the majority view with greater than proportionate probability. Jacobs & Campbell (1961) used Sherif's auto-kinetic task with the replacement method, described above, starting with confederates and ending with naive participants; they found that the conformity to exaggerated majority judgements was rapidly overwhelmed by people's trust in their individual perceptions. Thus, theirs was the first study to examine conformity from the cultural-evolutionary point of view and using the cultural-evolutionary definition. More recently, a series of experiments by McElreath et al. (2005; 2008) and Efferson et al. (2008) utilised a virtual 'farming' task in which participants choose to 'harvest' one of two crops. Each

crop had a stochastic payoff, and the optimal crop changed from time to time. Using variations on this design and model-fitting techniques, McElreath et al. (2005; 2008) concluded that individuals use a complex mix of payoff-biased and conformist learning, while Efferson et al. found individual differences, with some individuals using the conformity strategy and others ignoring frequency information. Finally, an experiment by Efferson et al. (2007) using a variation on this design with Bolivian pastoralists found little evidence for either conformism or payoff-bias; this experiment is remarkable for its unusual (compared to other studies) participant group, an important step towards drawing conclusions valid for the entire human species (see also the general survey by Henrich et al. (2010)).

What, then, are the population-level consequences of given social learning strategies? This question has been addressed through mathematical modelling since the books of Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985) and thus represents probably the most studied aspect of cultural evolution. The mathematical tools used to address this question are those relating to dynamical systems, both deterministic and stochastic, with the majority of models falling into the class of Markov chains (i.e. processes that evolve probabilistically in a way that depends only on their current state), usually analysed in discrete time-steps for ease of analysis.

Like in evolutionary biology (e.g. Kimura, 1984), cultural evolutionary researchers have realised the usefulness of constructing explicit neutral models in which individuals learn traits entirely 'at random', without the use of any particular social learning strategies or biases. Also like in evolutionary biology, there are a number of ways of conceptualising 'at random'. A series of 'random copying' models developed

by Bentley et al. (2004; 2007) assumes that individuals copy the trait of a random member of their population, finding that the resulting distribution of trait frequencies will follow a power law (that is, a distribution in which the most popular traits account for the majority of all traits, with successively less popular traits accounting for smaller and smaller proportions of all traits), and noting similar distributions in traits such as the frequencies of baby names and dog breeds. However, the statistical methods used in these papers to assess the fit of empirical evidence to the predictions of the models are unreliable (for a survey of this issue, see Clauset et al. (2009)). Later, Eriksson et al. (2010) proved 'Bentley's conjecture' that the rate of turnover in this model is almost independent of the size of the population. Strimling et al. (2009b) also have developed a variant of the model in which individuals may fail to learn a trait with some probability. Alternatively, Cavalli-Sforza & Feldman (1981) modelled the 'random drift' of continuous, rather than discrete, traits, characterising the rate at which populations would vary if each individual made a slight (additive) error during the learning process.

The effects of specific biases can be seen against the background of the expectations generated by neutral models. Initial models of content, model, and frequency-dependent biases were analysed by Boyd & Richerson (1985), partly with a view toward understanding their biological consequences. In particular, they found that conformist frequency-dependent bias leads to within-group homogeneity but between-group heterogeneity, a common phenomenon in humans (Boyd & Richerson, 1985). They also identified the possibility of 'runaway' co-evolution between model preferences and trait values, which may explain exaggerated phenomena such as whole-body tattoos in certain societies. More recently, Strimling et al. (2009a)

investigated the dynamics of content bias when the 'fitness' of a trait is partitioned into two components, 'diffusion' and 'retention', finding that the number of opportunities for learning was crucial in determining the evolutionary outcome, with traits with high 'retention' dominating only when individuals had a large number of opportunities for learning. Baldini (2013) investigated model biases, such as success- or prestige-bias, comparing the dynamics of strategies in which individuals averaged the success of all individuals with a certain trait with strategies in which individuals imitated the single most successful individual. He found that although there were many situations in which each strategy performed better than random copying, there were some situations in which each was worse than random copying: for the averaging strategy, this occurred when the optimal trait had high frequency in the population, and for the most-successful strategy when an on average suboptimal trait had a high variance in its outcomes. Mesoudi & Lycett (2009) investigated the effect of conformist and anti-conformist frequency-dependent biases on the distribution of trait frequencies, showing that conformity leads to distributions in which a small number of traits dominate others in frequency, and anti-conformity to distributions in which traits of intermediate frequency are favoured, both of which noticeably deviate from the power-law distribution noted above to result from random (unbiased) copying. Such models are very useful for understanding the detailed dynamics of cultural evolution.

These models lead to quantitative predictions and, conversely, allow inference from statistical data regarding a variety of traits. Researchers have also constructed and analysed models specific to certain classes of traits. Starting from Boyd & Richerson (1982; 1985), there has been a vibrant literature showing how human cooperative

tendencies may have arisen through a process of 'cultural group selection', i.e. group selection on groups differentiated by cultural traits (such as would be created by conformist bias, as noted above), and more recently researchers have applied the tools of evolutionary game theory to modelling cultural traits in situations where the utility of a certain trait depends on the traits adopted by other individuals, of which cooperation is a primary example (Boyd & Richerson, 2002; Peyton Young, 2011). Another set of processes of biological importance that have inspired cultural evolutionary models are the Neolithic and Industrial demographic transitions, where researchers have modelled the effects of technological and social change (e.g. the spread of contraception) on population sizes and compositions, both as individual traits (Fogarty et al., 2013) and in combination with other mediating traits (Ihara & Feldman, 2004; Borenstein et al., 2006). Thus cultural evolutionary models provide both general explanatory schemes for cultural change and specific explanations for important biological and social phenomena.

1.4. Discussion

Cultural evolution is now a burgeoning field, and much has been achieved. Much also remains to be done, and the preceding review suggests several obvious directions for future research. In general, there can never be too much replication, integration between theoretical and experimental studies, ecological validity in experiments, and realism in theories. The creation of detailed models of cognition, such as the Bayesian models noted above, which can be validated experimentally represents a fruitful line of research which currently has only been applied to relatively low-level cognitive processes. With respect to cumulative culture, it is still unclear exactly what cognitive and social factors allow humans but not other species to accumulate beneficial

cultural traits over time. The investigation of human social learning strategies and biases has shown that individuals show a good deal of heterogeneity in the biases they deploy, and that real life social learning strategies tend to be complicated and composed of mixtures of simple strategies; future experiments may investigate these complexities. Theoretical models have led to a detailed understanding of cultural evolutionary dynamics, and future research should attempt to base modelling assumptions on empirically validated observations and describe the interplay between multiple, interlocking biases and processes.

This thesis contributes to these aims in the following ways. In the second chapter, I describe an experiment investigating the effect of population size on cultural accumulation using a novel puzzle-making task. The third chapter constructs an explicit model for trait changes during transmission due to perceptual errors based on psychophysical principles, and tests this model experimentally with respect to Acheulean handaxe technology. The fourth chapter presents two models which extend previous theoretical investigations by incorporating multiple populations and linearly dependent cumulative traits, relating these models to empirical data on great apes and humans, and investigates how the models may shed light on the unique features of human culture. Finally, the fifth chapter investigates the possibility of giving a precise mathematical formulation to the concept of 'cultural selection', which thus far has been used in divergent ways in the literature, in a way analogous to R.A. Fisher's 'Fundamental Theorem of Natural Selection' in evolutionary biology, and therefore imposing some conceptual order on the various theoretical processes of cultural evolution.

Chapter 2.

An experimental demonstration of the effect of group size on cultural accumulation

This chapter was submitted to *Evolution and Human Behaviour*, where it received a 'revise-and-resubmit'.

This chapter was co-authored with Alex Mesoudi.

Abstract:

Cumulative culture is thought to have played a major role in hominin evolution, and so an understanding of the factors that affect cultural accumulation is important for understanding human evolution. One such factor that has been proposed is population size, with larger population sizes thought to be able to support more complex cultural traits. This hypothesis is supported by mathematical modelling and empirical studies of small-scale societies. However, to date there have been few experimental demonstration of this effect. Here we provide such a demonstration using a novel task, solving jigsaw puzzles. 80 participants divided into ten transmission chains solved puzzles in one of two conditions: individuals or groups of three. The mean number of pieces solved increased over time in the group condition, but not in the individual condition. Thus, our experiment provides support for the population size hypothesis and gives a demonstration of a factor underpinning complex cumulative culture.

2.1. Introduction

Cultural evolution is likely to have played a crucial role in hominin evolution. Examples of this include the spread of cooking and tool-use in earlier hominin species (Carmody & Wrangham, 2009; Foley & Lahr, 2003), and agriculture and writing in our own (Goody & Watt, 1963; O'Brien & Laland, 2012). Moreover, while social learning and cultural differences between populations are common in several non-human species (Galef & Laland, 2005), cumulative culture, defined as cultural traits that are dependent on other cultural traits (Boyd & Richerson, 1996; Enquist et al., 2011), may be unique to hominins (e.g. Dean et al., 2012). Cumulative culture is often characterised by the presence of traits that are too complex to have been invented by a single individual, instead having accumulated over multiple generations (Boyd & Richerson, 1996; Tomasello et al., 1993). Such traits are ubiquitous in human domains such as technology, science, and mathematics (Basalla, 1988; Hodgkin, 2005; Longair, 2003), and clearly played a crucial role in our current ecological success. Thus, an understanding of the factors that help or hinder the emergence of cumulative culture is important for understanding hominin evolution.

One factor that has been proposed to be related to the emergence and maintenance of cumulative culture is population size. In an influential paper, Henrich (2004) constructed a mathematical model providing a potential mechanism by which population size partly determines the cultural complexity attainable by that population. In Henrich's model, a population of a given size reproduces in discrete generations, and in each generation every adult member of the population acquires a cultural trait which can be more or less functional, the functionality being measured quantitatively. For example, the trait could be a bow-and-arrow, and its functional

measurement how far it shoots, or the trait could be a stone handaxe and its functional measurement how sharp it is. Each individual acquires the trait by copying the single individual in the previous generation with the most functional (i.e. 'best') version of the trait. However, they copy this individual imperfectly, so that most individuals make copying errors and acquire a version of the trait that is worse than that of their model, and a few individuals innovate successfully and acquire a version of the trait that is better than that of their model. This imperfect copying process is assumed to be random, so that each individual acquires a trait of different quality compared to other individuals.

Henrich (2004) showed that, given these assumptions, a population of a given size can maintain the transmission of a trait only up to a given functional level, or 'complexity'. Versions of the trait with greater complexity than the stable level will tend through transmission to get worse, and versions with lesser complexity than the stable level to improve, until the stable level is reached. This stable level increases with the size of the population, because the more individuals there are, the greater is the chance that large gains in functionality will occur through innovation and be copied by the next generation. In essence, more innovation takes place in larger populations. The stable level is of course determined by other factors in addition to the size of the population, most importantly its inherent complexity and difficulty to learn. Henrich's model has been extended by Powell et al. (2009; see also Shennan 2001) to look at population density and migration between sub-populations; by Mesoudi (2011a) to include the cost of acquiring more complex knowledge; and by Kobayashi & Aoki (2012) to the case of overlapping rather than discrete generations.

Empirical support for the link between population size and cultural accumulation is mixed. Henrich (2004) himself used his model to explain the loss of various technologies (e.g. complex bone tools, spears, boomerangs, fire-making) in Tasmania after rising seas cut it off from Australia approximately 11,000 years ago, thereby creating a smaller sub-population. Powell et al. (2009) used their extended model to explain the emergence of 'modern human behavior' (e.g. symbolic artefacts, complex tools, musical instruments) during the Pleistocene, noting that human population density in Africa, Europe and the Middle East was, according to estimates made using population genetic data and theory, similar at the times when these behaviours emerged. Four studies have investigated the relationship between population sizes of hunter-gathering and food-producing societies on the size and complexity of their toolkits. Collard et al. (2005) did not find a relationship in a sample of 20 hunter-gatherer populations mainly from North America; Kline & Boyd (2010) did find a relationship with both toolkit size and complexity among 10 Oceanic island populations; Collard et al. (2011) also did find a relationship with both toolkit size and complexity among 45 food-producing societies from around the world, but not among a similar sample of 34 hunter-gathering societies; and finally, Collard et al. (2013) similarly found a relationship with both toolkit size and complexity among 40 food-producing societies from around the world. At greater time depths, Lycett & von Cramon-Taubadel (2008) showed that Acheulean handaxe diversity fitted the predictions of a serial founder effect model, i.e. diversity decreased with predicted decreasing population size as early hominins migrated from an African origin (see also Lycett & Norton 2010). Thus, there is clearly some empirical support for a link between population size and cultural accumulation.

However, Henrich's (2004) model provides not only a population-level prediction – that cultural complexity should be dependent on population size – but also an individual-level mechanism underpinning that prediction. Regarding the latter, a crucial aspect of Henrich's model is that new, unknowledgeable individuals acquire their cultural knowledge from a single individual of the previous generation, and that this individual has the highest cultural complexity of their generation (i.e. individuals employ success-biased oblique cultural transmission). Under this mechanism, the population-size effect therefore works because larger populations are more likely, by chance, to contain highly successful individuals who are copied by the subsequent generation. While the assumption of success-biased cultural transmission is a reasonable one (see, for example, McElreath et al. 2008; Mesoudi, 2008, 2011c), learning from just a single individual may be less plausible. Indeed, Enquist et al. (2010) found analytically that cultural transmission from multiple individuals is more likely to maintain knowledge in a population than learning from a single individual, albeit in a non-cumulative cultural system. One might expect that learning from multiple skilled individuals, and combining their knowledge in each generation, would be at least as effective a mechanism for maintaining and accumulating complex cultural knowledge than relying on just the most-skilled individual, particularly when such knowledge can be easily combined. Under this alternative mechanism, then, the population-size effect outlined by Henrich (2004) would still occur, but would occur instead because in larger populations, there are more models available from whom knowledge can be additively combined.

While archaeological and paleoanthropological studies of the kind described above can address the general prediction of cultural-demographic models (a positive

relationship between population size and cultural complexity), they cannot test the validity of the underlying mechanism responsible for this effect, given that we cannot directly observe cultural transmission dynamics in long-dead populations (e.g. whether people typically copied one or more individuals, or whether they copied successful individuals). As such, even though there is general support for the link between population size and cultural complexity, this may not necessarily be through the mechanism assumed in existing models. To probe such mechanisms, laboratory experiments are needed, in which cultural transmission dynamics can be directly observed and factors can be isolated and their effects precisely measured (Mesoudi & Whiten, 2008).

To date, three studies have experimentally tested the link between population size and cultural accumulation. Caldwell & Millen (2010) asked participants to build paper airplanes that would fly as far as possible, with participants observing either one, two, or three previous participants building their paper airplanes as well as those participants' completed airplanes. They did not find that the distance the airplanes flew increased more rapidly or to a higher level as the number of models increased. Derex et al. (2013) had groups of 2, 4, 8 or 16 participants design computer-generated arrowheads (a simple trait) and fishing nets (a complex trait), allowing participants to copy the design of one other participant given information about other participants' success. Derex et al. found that only in the two larger groups (8 and 16) were the simple designs improved, and the complex designs maintained, over successive generations. Finally, Muthukrishna et al. (2014) had chains of participants - either one per generation or five per generation - draw a symbol using a complex graphics software package, or tie a complicated knot. Written instructions, final products

and/or videotaped behaviour were transmitted between generations. As predicted, the symbols drawn by chains of five participants increased in complexity due to increasingly effective instructions compared to the chains of single participants, and the knots tied by chains of five participants were more likely to be maintained than the knots tied by the chains of single participants.

Derex et al. (2013) and Muthukrishna et al. (2014) therefore provide support for the overall prediction that cultural complexity is more likely to be maintained and accumulated in larger groups, although Caldwell & Millen (2010) found no effect. Regarding the mechanism, both Derex et al. (2013) and Muthukrishna et al. (2014) found that Henrich's (2004) assumption of success-biased transmission from a single model is a plausible means by which the population-size effect works. However, none of these studies provided a proper test of the alternative mechanism outlined above, where information is integrated from multiple sources. Derex et al. (2013) only allowed participants to learn from a single person at a time, given information about other participants' relative success. Muthukrishna et al. (2014) allowed the five-per-generation participants to view the solutions of all five previous participants simultaneously, potentially allowing the integration of multiple participants' knowledge, but in practice participants predominantly copied the single most successful participant of those five. Caldwell & Millen's (2010) participants could also view two or three models simultaneously, but the task used, building paper airplanes, was not conducive to integrating information across models because different airplane designs may be incompatible. That is, combining elements of two different designs may sometimes lead to a better design, but often to an even worse design. The tasks used by Derex et al. and Muthukrishna et al. - making fishing nets

and tying knots - similarly have solutions that are difficult to combine. Interestingly, a recent study by Eriksson & Coultas (2012), looking at the cultural transmission of written texts, found that more information was preserved during transmission when each generation had access to two previous participants' recall, compared to one previous participant's recall. While not designed as a test of cultural accumulation or the cultural-demographic models reviewed above, Eriksson & Coultas' study provides some support for the notion that having access to multiple cultural models can at least maintain information in a population better than having access to just a single model.

Our aim in this study is to explicitly test the population size hypothesis for cultural accumulation along the lines of previous experimental studies, but with a task – completing jigsaw puzzles – in which observations from multiple models can be easily combined into one solution. We compare transmission chains composed of a single individual per generation with chains composed of three individuals per generation, with the latter able to see the partially-completed puzzles of all three members of the previous generation simultaneously. If our prediction is upheld – that the three-participants-per-generation chains are more likely to accumulate knowledge (in the form of proportion of the puzzle completed) than the one-participant-per-generation chains – then this would suggest an additional mechanism by which population size influences cultural complexity to the one-parent success-biased cultural transmission currently assumed by population-demographic models and tested in previous experiments.

2.2. Methods

2.2.1 Participants

80 unpaid participants, undergraduate students at the Universities of Durham and Exeter, took part as part of their undergraduate courses. Ethical permission for the experiment was given by the Research Ethics and Data Protection Committee, Department of Anthropology, Durham University, and all participants read and signed informed consent forms.

2.2.2 Task and design

The experimental task was to complete a jigsaw puzzle. The puzzle had 100 pieces and measured 33.5cm by 45cm; the puzzle picture can be seen in Fig. 2.1. Participants were divided into 10 transmission chains, 5 in each of two conditions: *individuals* and *groups* of three (Figure 2.2). Each transmission chain had four non-overlapping generations. Each participant was asked to complete as much of the puzzle as possible in 12 minutes, starting from scratch. (The written instructions were: ‘You have 12 minutes to complete a jigsaw puzzle. Complete as much as you can.’). Participants were not given a photo of the completed puzzle to help them; however, in generations after the first, participants were able to see the partially-completed puzzles created by the participants in the generation before them. In the group condition, each of the three participants in one generation sat next to each other, but were divided by screens that obscured each others’ puzzles, and they did not interact in any way. Before being presented to successive generations, all loose single pieces were removed from partially-completed puzzles, but the physical layout of completed pieces was not altered or standardised.



Figure 2.1. The painting on the jigsaw puzzle. Image by John Francis; used with the kind permission of the copyright holder, Gibsons Games.

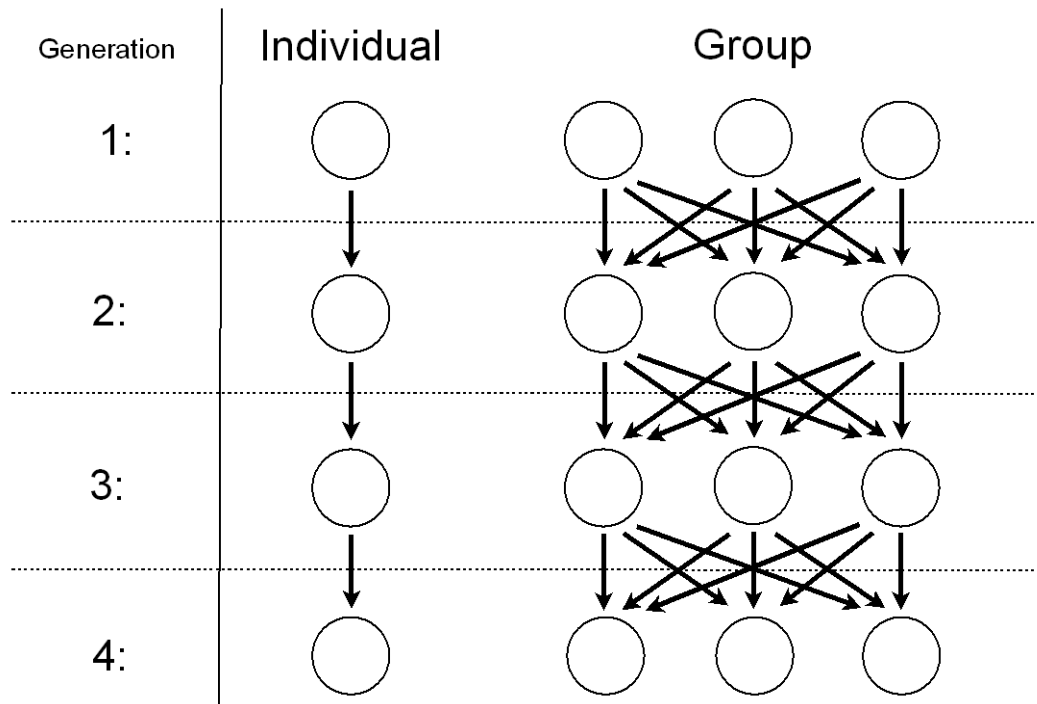


Figure 2.2. An illustration of the experimental design. There were 5 replicate chains in each condition, giving 10 chains in all.

The outcome measure for each participant was the number of puzzle pieces that they correctly connected to at least one other puzzle piece. Sets of completed puzzle pieces did not need to form one large set to be counted; multiple small sets of completed pieces contributed in the same way to the outcome measure. In the group condition, we also measured the number of distinct puzzle pieces correctly connected to at least one other puzzle piece across all three puzzles completed by the participants in each generation. This gives a measure of the amount of information about the puzzle that the succeeding generation was able to observe, accounting for the duplication of completed pieces across different observed puzzles.

2.3. Results

The results of the experiment can be seen in Fig. 2.3. It is visually evident that the mean number of pieces completed trends upward in the group condition but not in the individual condition. To test this hypothesis statistically, we used Page's (1963) trend test, which tests for a hypothesised ordered monotonic trend (in this case, an increasing trend) in the means of a number of different treatments (which are generations in this case). The test was non-significant ($L_{5,4} = 123, p > 0.05, n = 20$) for the individual condition, and significant ($L_{5,4} = 141, p = 0.01, n = 20$) for the group condition. We also compared the means of the first and last generations in each condition using Welch's two-sample t -test: for the individual condition there was no significant change in the number of puzzle pieces connected ($t_{6,1} = 0.2422, p = 0.5917$, one-sided, $n = 10$), while for the group condition there was ($t_{23,2} = -2.2882, p = 0.0158$, one-sided, $n = 30$), with more pieces connected by the final than first generation.

As can be seen on Fig 2.3a, the last generation contained outliers in both one group condition chain and one individual condition chain, and to ensure the robustness of the trend we also applied Page's trend test to the data with these outliers replaced by the mean value of the other chains in the respective conditions in the last generation. The test was again non-significant ($L_{5,4} = 128.5, p > 0.05, n = 20$) for the individual condition, and significant ($L_{5,4} = 137, p < 0.05, n = 20$) for the group condition.

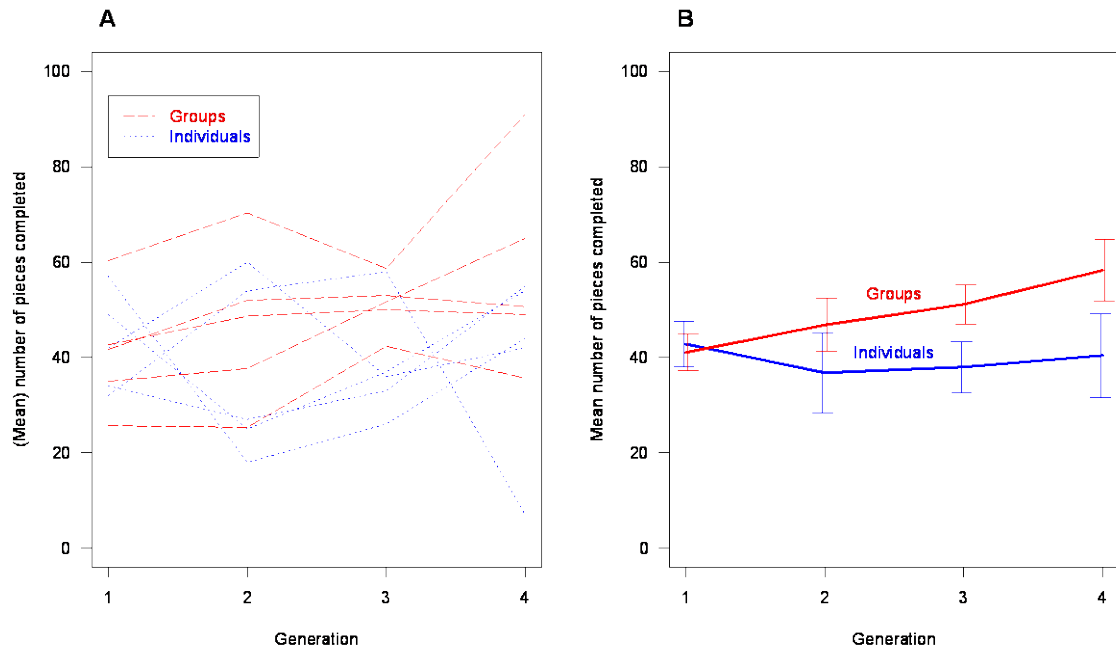


Figure 2.3. The results of the experiment. (A) The number of pieces completed in each individual chain in both conditions. Each datapoint for the group condition shows the mean number of completed pieces across the three participants in that group. The full dataset is available in Appendix A. (B) Mean number of pieces completed in each condition. The error bars show standard errors.

The number of distinct pieces completed in the three puzzles of each group is shown in Fig. 2.4. As with the mean number of pieces completed, this appears to trend upwards, and indeed Page's trend test showed a significant increasing trend ($L_{5,4} = 139, p < 0.05, n = 20$).

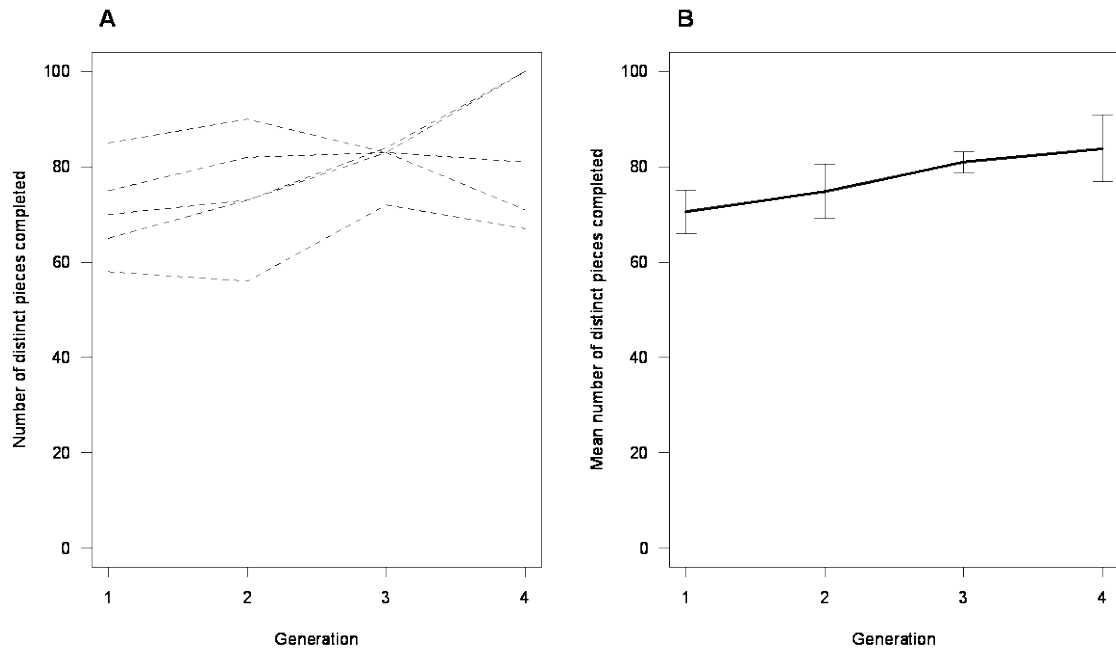


Figure 2.4. The number of distinct pieces completed in the group condition. (A) Number of distinct pieces completed in each chain. The full dataset is available in Appendix B. (B) Mean number of pieces completed. Error bars show standard errors.

2.4. Discussion

Our experiment showed no increasing trend in the mean number of jigsaw pieces completed in the individual condition, when each generation of the transmission chains was a single individual, but a significant increasing trend in the group condition, when each generation consisted of three individuals. The larger number of individuals is clearly able to maintain the transmission of a greater amount of information about the puzzle. Thus, the results of the experiment support the proposed link between population size and cultural accumulation put forward by Shennan (2001), Henrich (2004), Powell et al. (2009) and others.

The upward trend in the number of distinct pieces completed across a group shown in Fig. 2.4 suggests that participants were integrating information from

multiple models, as predicted. This therefore provides an alternative mechanism by which the population-size effect operates, in addition to the success-biased cultural transmission from a single demonstrator assumed in previous models (e.g. Henrich 2004) and tested in previous experiments (e.g. Derex et al., 2013). Our finding supports recent modelling (Enquist et al., 2010) and experimental (Eriksson & Coultas, 2012) work showing the benefits of multiple cultural parents on cultural transmission, although extended here to a cumulative cultural context.

It is instructive to compare our results with those of Caldwell & Millen (2010), who found no effect of group size despite similar group sizes and generations. As discussed in the Introduction, different tasks will be more or less conducive to cultural accumulation. In our jigsaw puzzle task it is easy to combine information from multiple different puzzles completed by members of a previous generation into one's own puzzle. By contrast, information about multiple different paper airplane designs may conflict, and combining multiple designs may lead to a worse design than any of the models. While copying the single airplane design of the most successful individual may be effective in larger groups or over more generations than were employed by Caldwell & Millen, the fact that we observed accumulation with similar group sizes and generations suggests that combining knowledge from multiple cultural sources can be an equally potent mechanism for cultural accumulation compared to copying a single successful individual, given the appropriate task.

Our experiment shows that the characteristics of the task are important in determining the extent to which population size will affect its cultural accumulation, and future modelling work on the relationship between population size and

cumulative culture should take into account not only factors extrinsic to the task but also factors intrinsic to it. One way of conceptualizing task differences is by considering uni-modal vs. multi-modal utility, or ‘fitness’, landscapes (see Mesoudi 2008; Mesoudi & O’Brien 2008a,b). The task of finishing a jigsaw puzzle constitutes a unimodal, single-peaked utility landscape, because the more pieces a participant has completed, the closer to completion they are; in our experiment, it did not matter which particular combination of, say, 40 pieces was completed, so long as the number was 40. However, the task of building paper airplanes may create a multimodal, multi-peaked utility landscape, in which there are multiple locally optimal designs that can solve the task relatively well (though there may be a single globally optimal design). These multiple designs may be rather distinct from each other, and designs which mix features of two or more ‘good’ designs may fall into a utility valley and be relatively inefficient at solving the task.

It may be that there is a continuum along which real-world technologies can be placed, from simple utility landscapes with one peak to complex utility landscapes with very many distinct peaks of quite unequal height. An engineering correlate of this continuum may be the extent to which the technology consists of independent vs. interdependent parts. Moreover, these differences may occur at different levels of granularity. For example, complex post-Industrial Revolution technologies such as cars and computers incorporate large numbers of different parts, which must work together in order for the technology to function. However, if a certain part is required for a specific task, it may not matter exactly how it achieves that task, and so the overall functioning of the technology (e.g. car) may be relatively independent of the exact mechanism in which the constituent part fulfills its function (see Arthur, 2009).

Another example of such hierarchical structure is found in modern computer software, which is often written using ‘object-oriented’ and ‘functional’ techniques in which the external behavior of various system sub-parts is highly constrained but the internal implementation of these sub-parts is relatively unconstrained (Mitchell, 2002).

Future experiments and empirical work may provide more evidence on what tasks are particularly conducive to the build-up of cumulative culture, the way in which independence and interdependence of technological sub-components affects technological accumulation, and allow us to ‘measure’ the fitness landscape of a given task. A promising path may be to use experimental tasks with direct ecological validity to a specific domain, such as mathematics, tool-use, or construction, unlike the tasks used here and in other recent experiments, which require little specialist knowledge. Such experiments may help to show whether certain domains are more amenable to cultural accumulation than others. Another path may be to examine the contribution of collaboration, which was not possible in our experiment, to cumulative culture. More refined experimental designs would allow this factor to be isolated, comparing in effect the ‘between-generation’ and ‘within-generation’ components of cultural accumulation. Experimental work such as this can then be used to inform historical, anthropological and archaeological data, to make specific predictions regarding which kinds of cultural traits are most likely to have been impacted by demography, and thus provide substantial insight into human biological and cultural evolution.

Chapter 3.

An experimental test of the accumulated copying error model of cultural mutation for
Acheulean handaxe size

This chapter was co-authored with Stephen J. Lycett and Alex Mesoudi.

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Abstract:

Archaeologists interested in explaining changes in artifact morphology over long time periods have found it useful to create models in which the only source of change is random and unintentional copying error, or ‘cultural mutation’. These models can be used as null hypotheses against which to detect non-random processes such as cultural selection or biased transmission. One proposed cultural mutation model is the accumulated copying error model, where individuals attempt to copy the size of another individual’s artifact exactly but make small random errors due to physiological limits on the accuracy of their perception. Here, we first derive the model within an explicit mathematical framework, generating the predictions that multiple independently-evolving artifact chains should diverge over time such that their between-chain variance increases while the mean artifact size remains constant. We then present the first experimental test of this model in which 200 participants, split into 20 transmission chains, were asked to faithfully copy the size of the previous participant’s handaxe image on an iPad. The experimental findings supported the model’s prediction that between-chain variance should increase over time and did so in a manner quantitatively in line with the model. However, when the initial size of the image that the participants resized was larger than the size of the image they were copying, subjects tended to increase the size of the image, resulting in the mean size increasing rather than staying constant. This suggests that items of material culture formed by reductive versus additive processes may mutate differently when individuals attempt to replicate faithfully the size of previously-produced artifacts. Finally, we show that a dataset of 2601 Acheulean handaxes shows less variation than predicted given our empirically measured copying error variance, suggesting that

other processes counteracted the variation in handaxe size generated by perceptual cultural mutation.

3.1. Introduction

The idea that human culture – defined here as socially transmitted information such as beliefs, knowledge, skills, artifact designs, and customs – constitutes an evolutionary process was hinted at by Darwin himself in *The Descent of Man*, where he suggested that languages evolve over time in a manner analogous to the diversification and extinction of biological species (Darwin, 1871). This notion of cultural evolution was explored further throughout the twentieth century by archaeologists (Binford, 1963; Clarke, 1968), anthropologists (Sahlins & Service, 1960; Schwartz & Mead, 1961) and psychologists (Gerard et al., 1956; Campbell, 1975), but it was not until the work of Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985) in the 1980s that the implications of the parallels between biological and cultural change were more rigorously explored using the same quantitative mathematical modelling techniques that population geneticists use to successfully model and understand biological evolution (see Mesoudi, 2011a esp. chap. 3). Our focus here is on the application of these cultural evolutionary methods and concepts to archaeology (O’Brien & Lyman, 2002; Shennan, 2011), which can be seen as the ‘cultural equivalent’ of paleobiology in its aims to document and explain past evolutionary change (Mesoudi et al., 2006). This has included the use of phylogenetic methods to reconstruct historical relationships between artifacts (O’Brien et al., 2001), the use of models originally developed in population genetics, such as serial founder effect and neutral drift models, to explore the effects of demography on artifact variation (Lycett, 2008; Lycett & von Cramon-Taubadel, 2008; Neiman, 1995; Shennan & Wilkinson, 2001; Bentley & Shennan, 2003; Bentley et al., 2004; Kohler et al., 2004; Schauer, 2009; Steele et al., 2010; Brantingham & Perreault, 2010), and the explanation of artifact

variation in terms of cultural transmission biases such as prestige bias or conformity (Kohler et al., 2004; Bettinger & Eerkens, 1999).

Another important process of cultural evolution that may have fruitful application in archaeology is cultural mutation. By analogy to genetic mutation, this describes the process in which ideas are involuntarily changed when they are transmitted from one person to another. In this study we present the first explicit experimental simulation of a model of cultural mutation in archaeology. Specifically, we are interested in testing the accumulated copying error (ACE) model proposed by Eerkens & Lipo (2005), in which random error in a quantitative artifact dimension (e.g. size or thickness) is generated by the physiological limitations of the hominin perceptual system. Eerkens & Lipo drew on experimental findings from psychophysics which showed that the accuracy of human perception has physiological limits, especially our ability to perceive differences between objects (Coren et al., 1994). If the difference in size between two objects is below some threshold, then this size difference will tend to be imperceptible to the naked human eye, and this will become more and more likely as the size difference between the objects grows smaller. Such error thresholds are always relative to the size of the object, rather than absolute. For example, two lines that are less than 3% different in length are typically perceived as identical, with this 3% value known as the Weber fraction for this particular dimension (line length). Eerkens & Lipo applied this basic principle of psychophysics to the repeated cultural transmission of artifacts. They assumed that when attempting to copy the morphology of an artifact as faithfully as possible, and in the absence of formal measurement aids (e.g. rulers), the manufacturer is likely to make small copying errors that are imperceptible to them due to the aforementioned perception thresholds. If that

person's copied artifact is in turn copied by another person, and so on along a transmission chain, then copying errors will compound over time, possibly creating significant morphological change compared to the original artifact. Moreover, if multiple such transmission chains evolve independently, then the variation between these diverging chains is likely to become substantial and to increase over time. Note that this process will take place regardless of whether any other cultural evolutionary forces are at work, and thus, it may be useful to incorporate this model of mutation in other, more complicated models.

Eerkens & Lipo presented a simple simulation model of this process in which a continuous trait value is transmitted over successive generations of individuals with a 3% random normal error rate, and with 10 independently evolving chains. Their simulation showed that, as expected, the independent chains diverged over time as some became larger and others became smaller. Due to the randomness of the error, the overall mean value did not change over time, while the between-chain variation did increase over time. They then applied these expectations to two case studies, showing that the thickness of Owens Valley projectile points increases in variation in a way consistent with the random accumulated copying error model, while the basal width of those points, and the vessel diameter and thickness of Late Woodland pots, show less variation than expected, suggesting that some non-mutation process (e.g. conformist transmission) may have been at work in these latter cases.

Our aim here is to provide an explicit experimental test of Eerkens & Lipo's ACE model of artifact transmission. Although the assumptions of their model are based on previous experimental findings from psychophysics (Gilinsky, 1951), from where

their 3% copying error assumption is derived, it is unclear (i) whether this 3% error threshold is uniform across a large population of individuals, or whether there is inter-individual variation in this threshold value (especially given previous findings of substantial individual variability in some perceptual psychometric functions: Coello & Garriga, 1991; Engeland & Dawson, 1974), and thus how any inter-individual variation affects the robustness of the model; (ii) whether this 3% threshold, originally obtained for simple lines or abstract geometric shapes, also applies to more realistic artifact shapes; and (iii) whether it is valid to simply extrapolate a single individual's perceptual error along successive transmission episodes, or whether there are unexpected dynamics introduced by the compounding of individual errors (Hamilton & Buchanan, 2009, for example, argued that the compounding of errors causes the size of artifacts in chains to decrease, on average).

To address these issues, we asked multiple chains of participants to copy an artifact image as faithfully as they could, in a direct replication of Eerkens & Lipo's model. In addition, in order to provide an explicit model within which to insert our experimentally-derived copying-error parameter, we also derive two formal mathematical predictions of the model which allow us to test the assumptions of the model with our data. Although this is the first experimental test of a cultural *mutation* model of artifactual evolution, it adds to a handful of other studies that have experimentally simulated cultural transmission dynamics in the archaeological record (e.g. Mesoudi & O'Brien, 2008).

Although the findings of our experimental simulation, like Eerkens & Lipo's original model, are in principle applicable to any culturally transmitted artifact, we take a

particular interest here in the question of size variation in Acheulean handaxes.

Acheulean handaxes were used by various hominin species from at least 1.76 million years ago (Lepre et al., 2011) to at most 0.14-0.12 million years ago (Haslam et al., 2011), and were thus used longer than all other known hominin tools apart from Oldowan artifacts (Gowlett, 2011). They were used in Africa, Europe, and Asia, and their temporal span witnessed the evolution of several new hominin species (Clark, 1994; Klein, 2009). Given this extended temporal and geographic spread, it is perhaps unsurprising that patterned variation *within* this technocomplex has been detected in statistical analyses of handaxe shape (e.g. Lycett & Gowlett, 2008). However, it has also been argued that certain patterns of stability in handaxe form and size (at least within certain bounds) over this temporo-geographic spread might reflect culturally selective constraints for functional or social reasons (Kohn & Mithen, 1999; Vaughan, 2001; Gowlett, 2006; Gowlett, 2009). Applying and testing explicit models of evolution by cultural mutation will allow us to investigate the question of handaxe size in a rigorous way, and provide a base for future explicit models of their cultural selection (e.g. for functional or social purposes). As chimpanzee visual acuity is similar to modern human visual acuity (Matsuzawa, 1990), it is likely that hominin species would have had similar visual acuity to our modern human participants, and thus that our measured parameters will be similar to those of fossil hominins. Thus, knowledge of the parameters can be used to derive predictions about the amount of variation generated during the temporal span of Acheulean handaxes that we should expect to find in the archaeological record under the ACE model, and thereby connect our microevolutionary experiment to documented macroevolutionary patterns. We therefore use a handaxe image as our 'experimental artifact' in the present study, and

in the Discussion we ask whether the experimentally-informed ACE model can account for observed patterns of Acheulean evolution.

3.2. Methods

3.2.1. Model

The ACE model postulates that each chain consists of a number of generations, each of which has one member. In each generation, the sole member copies some continuously-valued attribute of the artifact of the sole member of the previous generation, introducing a randomly determined quantity of copying error. As we expect each member to have a similarly-shaped distribution of copying errors, the Central Limit Theorem justifies modelling the random determination of copying error as drawing a random deviate from some normal distribution. The famous psychophysical finding of Weber's Law, namely, that perceptual errors scale proportionally to the magnitude of the attribute of the object being perceived, rather than being fixed, absolute quantities, justifies multiplying the previous generation's value by the randomly sampled copying error, rather than adding the copying error to the previous generation's value.

Thus, we write:

$$S_g = S_{g-1}\varepsilon_g,$$

where S_g is the value at generation g , S_0 is the starting value of the process, and

$\varepsilon_1, \varepsilon_2, \dots, \varepsilon_g$ are i.i.d. random variables equal to $N(1, \sigma^2)$. We are interested in the

moments of S , so that we can compare empirical measurements of summary statistics

with the model's predictions. Since S_g is simply $S_0 \prod_{i=1}^g \varepsilon_i$, and the error variables are

both independent and identically distributed, we can see that:

$$\mathbb{E}(S_g) = \mathbb{E}(S_0 \prod_{i=1}^g \varepsilon_i) = S_0 \mathbb{E}(\prod_{i=1}^g \varepsilon_i) = S_0 \prod_{i=1}^g \mathbb{E}(\varepsilon_i) = S_0 \prod_{i=1}^g 1 = S_0,$$

so the expectation of S is always equal to its starting value. As for the variance:

$$\begin{aligned} \text{Var}(S_g) &= \mathbb{E}((S_g - \mathbb{E}(S_g))^2) = \mathbb{E}((S_g - S_0)^2) = \mathbb{E}(S_g^2 + S_0^2 - 2S_g S_0) \\ &= \mathbb{E}(S_g^2) + S_0^2 - 2S_0 \mathbb{E}(S_g) = \mathbb{E}((S_0 \prod_{i=1}^g \varepsilon_i)^2) - S_0^2 = \mathbb{E}(S_0^2 (\prod_{i=1}^g \varepsilon_i)^2) - S_0^2 \\ &= S_0^2 \mathbb{E}(\prod_{i=1}^g \varepsilon_i^2) - S_0^2 = S_0^2 (\prod_{i=1}^g \mathbb{E}(\varepsilon_i^2) - 1) = S_0^2 (\prod_{i=1}^g \mathbb{E}(\varepsilon_1^2) - 1). \end{aligned}$$

We can find $\mathbb{E}(\varepsilon_1^2)$ by noting that:

$$\begin{aligned} \sigma^2 &= \text{Var}(\varepsilon_1) = \mathbb{E}((\varepsilon_1 - \mathbb{E}(\varepsilon_1))^2) = \mathbb{E}((\varepsilon_1 - 1)^2) = \mathbb{E}(\varepsilon_1^2 + 1 - 2\varepsilon_1) \\ &= \mathbb{E}(\varepsilon_1^2) + 1 - 2\mathbb{E}(\varepsilon_1) = \mathbb{E}(\varepsilon_1^2) - 1, \end{aligned}$$

and thus $\mathbb{E}(\varepsilon_1^2) = \sigma^2 + 1$, allowing us to find the variance:

$$\text{Var}(S_g) = S_0^2 (\prod_{i=1}^g \mathbb{E}(\varepsilon_1^2) - 1) = S_0^2 (\prod_{i=1}^g (\sigma^2 + 1) - 1) = S_0^2 ((\sigma^2 + 1)^g - 1).$$

Both of these moments are the moments of a random variable that represents an individual chain, and are therefore unobservable; however, we can estimate them by measuring the mean and sample variance of multiple independently evolving chains, expecting that the mean will stay constant over time and the sample variance will increase without bound. 10 such chains, evolving for 400 generations, are shown in Figure 3.1A, along with their predicted mean and variance. This partially recreates the results of Eerikens & Lipo (2005). While our analysis confirms that the mean should not change over time, our results suggest that the variance should increase exponentially, rather than plateau. However, when σ is small (e.g., within the typical range for human copying error distributions) then both our and their equations give very similar predictions for the variance.

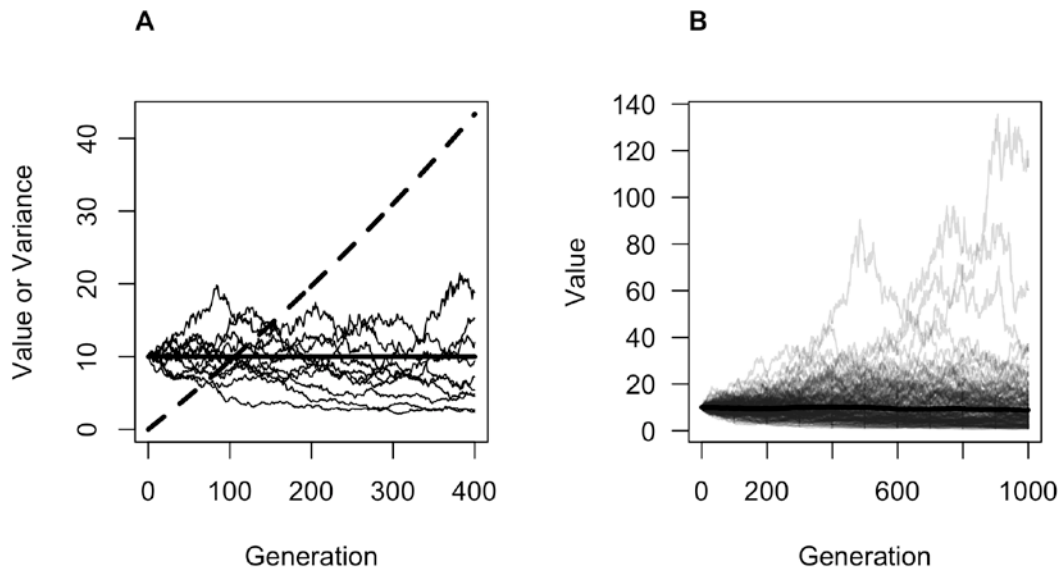


Figure 3.1. Simulations of the ACE model. (A) 10 chains evolving over 400 generations (black lines) and theoretically predicted mean (thick black line) and variance (thick dashed line). (B) 200 chains evolving over 1000 generations, with individual chains represented by semi-transparent grey lines so that multiple overlapping lines produce darker colors. The thick black line shows the mean of all chains. In both panels, $S_0 = 10$ and $\sigma = 0.03$.

We also note that our model and results deviate slightly from a more recent ACE model presented by Hamilton & Buchanan (2009). They found that, in contrast to both Eerks & Lipo and ourselves, accumulated copying error causes the mean to become smaller. They argued that this is because, given that copying error is relative to the size of the object being transmitted, chains with artifacts that happen to get smaller will also have smaller copying error, making them less likely to deviate further and more likely to remain small. In contrast, chains with artifacts that happen to get larger will have larger copying error, increasing the probability that they will eventually produce smaller objects over time. Our results, however, suggests that this is not the case: while it is true that most chains of artifacts get smaller because small

chains of artifacts stay small, pushing the mean down, this is counterbalanced by a minority of chains of artifacts that get much larger. Because copying error is relative, those large chains get exponentially large. In other words, small chains of artifacts stay small, and most chains of artifacts become small, but large chains of artifacts get much, much larger, with the overall mean not changing. This can be seen in Figure 3.1B, which shows the value of most chains of artifacts drifting smaller than the starting value, a few chains of artifacts drifting to extremely high values, but the mean of all chains of artifacts staying basically constant through time. The difference between these results may be due to Hamilton & Buchanan's use of log values, which will reduce the effect of these very large values.

Note that one obvious objection to the above analysis is that normal distributions can take on any value, including negative values, and thus that the resulting values of \mathcal{S} can be negative, which is nonsensical in many interpretations, e.g. if \mathcal{S} represents size or weight. This is a valid objection in general, but as human perceptual error distributions tend to have very low variance - for example, as we show later, in our data $\sigma \approx 0.03$ - it makes negligible difference for cultural drift models. For instance, substituting a truncated normal distribution bounded below at 0 with $\sigma = 0.03$ into the equations above gives $\mathbb{E}(\varepsilon) \approx 1 + 10^{-240}$, an astronomically small difference that would not affect predicted means and variances even after millions of generations.

3.2.2. Experiment

In our experiment, we wish to (1) estimate σ^2 , the variance of the distribution of copying errors, and (2) test whether the mean and sample variance of multiple independently evolving chains in an experimental setting match their expected values.

Ideally, we would do this by running multiple transmission chains in which participants would be asked to create a new Acheulean handaxe by faithfully copying the previous participant's handaxe. However, Acheulean stone knapping is both dangerous and difficult (Whittaker, 1994; Edwards, 2001), and finding enough participants who would be both willing and able to knap handaxes would be a challenge. Thus, we settled on a compromise that allowed us to simulate the essential features of the model: an electronic, touch-screen-based resizing task. Using an iPad, each participant in each transmission chain was shown the previous participant's handaxe and asked to resize a second handaxe to match the size of the previous participant's as closely as possible (Figure 3.2). This resizing was done using a pinching gesture with two fingers on the iPad screen, and as much time was given as needed; thus, we feel justified in assuming that manufacturing error, as opposed to perceptual error, was not a significant factor in the results of the experiment. It should be emphasized that our transmission-chain experiment thus focuses solely on the ability of participants to replicate the attribute of artifact *size*, to the exclusion of shape attributes.

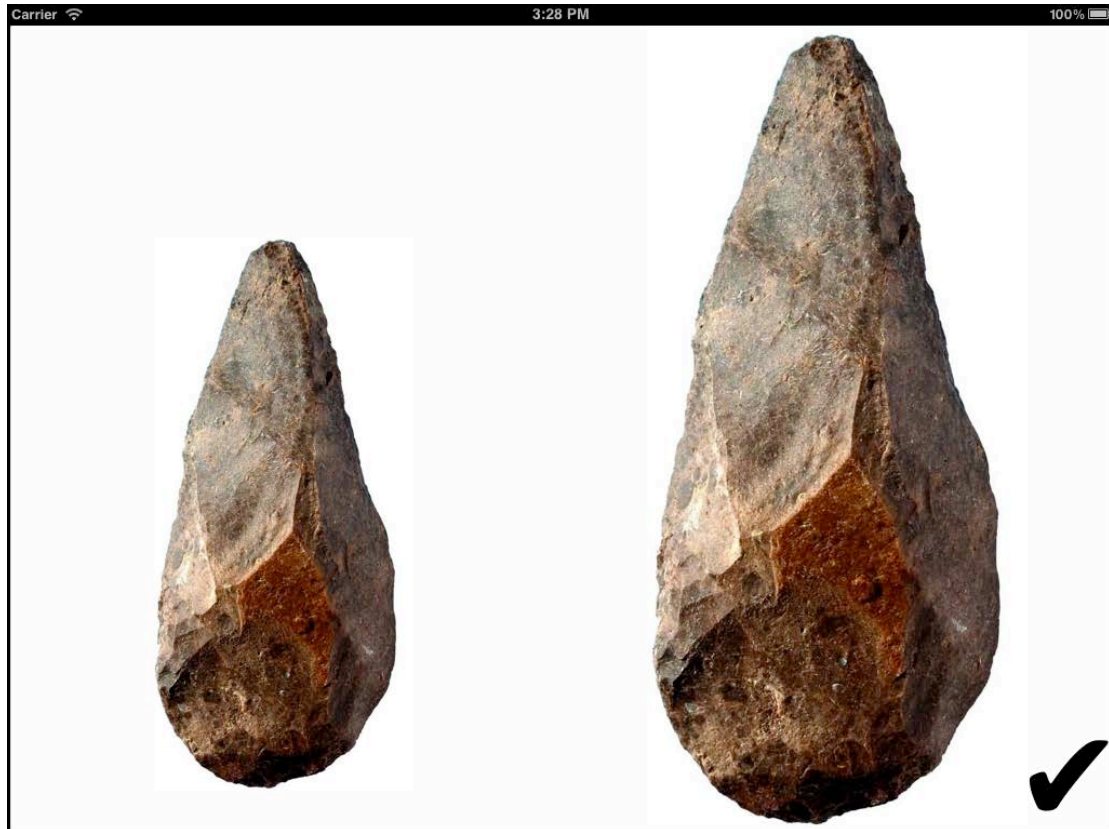


Figure 3.2. The main screen of the iPad-based experiment. The handaxe image on the left was created by the previous participant, and the current participant is asked to resize the handaxe image on the right so as to match the size of the previous participant's as closely as possible. Participants pressed the tick mark to complete the experiment.

In our experiment, then, the continuous value modelled as S in our model is the size of the handaxe, with height and width scaled isometrically. As the right-hand handaxe image (the one that is to be resized by the participant) must begin at some arbitrary size, we ran two conditions of the experiment: one in which the right-hand image began at the maximum possible size (i.e. with the same height as the screen, 14.4 cm), and one in which it began at 1/3 the size of the screen (4.8 cm height). The zeroth-generation left-hand side handaxe image in each transmission chain was set at 10 cm height (i.e., $S_0 = 10$), and the width of all images was always 7/15 of their height.

We ran 10 transmission chains with 10 participants each in both conditions. All participants were distinct, i.e., no participant took part in more than one chain or more than once within a chain. Participants were recruited primarily by soliciting in the library of Queen Mary, University of London. 59.5% were female and 75.5% were within 18 and 25 years of age. Those participants who wore corrective eyeglasses or contact lenses were allowed to keep them on for the experiment.

3.2.3. Ethics statement

The study was approved by the Queen Mary Research Ethics Committee. All participants viewed an informed consent screen and agreed to it by tapping an electronic button; this procedure was approved by the Research Ethics Committee. All data was analyzed anonymously, and sex and age information was deleted after calculating summary statistics across the whole sample.

3.3. Results

Our full results dataset is available in Appendix C. Our first aim was to estimate σ^2 . Figure 3.3 shows normal probability plots (in which a straight diagonal line at $y = x$ indicates perfect fit to a normal distribution) for the distribution of empirically measured copying errors in each condition. For each transmission event, copying error is measured by the final size of the right hand image divided by the size of the left hand image. As can be seen, they appear normal; in order to formally test this hypothesis, we used the Anderson-Darling normality test, which did not reject normality for either distribution (larger-axe condition: $A = 0.53$; $p = 0.17$; smaller-axe condition: $A = 0.44$; $p = 0.29$). Having established the condition's normality, we can estimate σ by measuring the sample standard deviation (we report the sample

standard deviation here rather than the sample variance to avoid reporting very small numbers, and also because standard deviations are easier to interpret, being measured in physical units rather than units squared), which was 0.0269 for the larger-axe condition and 0.0399 for the smaller-axe condition, with an overall mean of 0.0343.

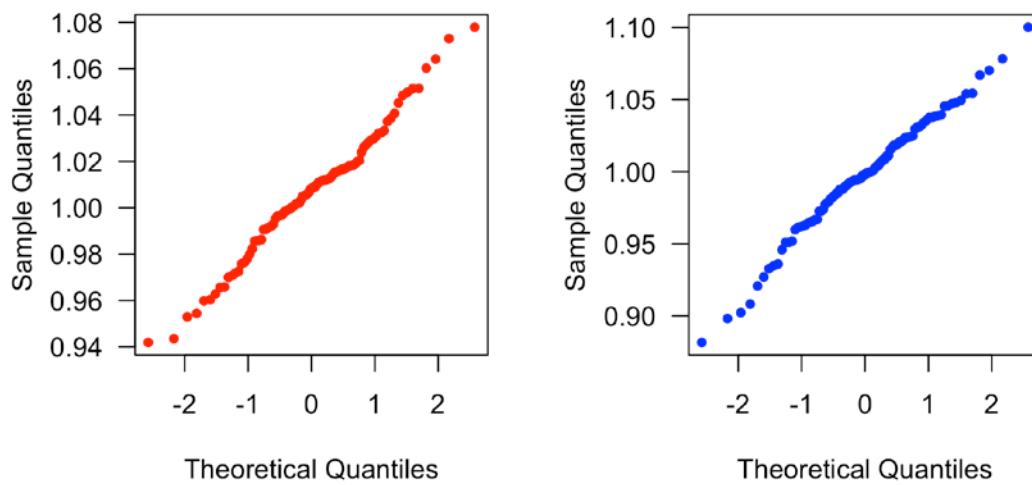


Figure 3.3. Normal probability plots of empirically measured copying errors. Data from the condition with the larger initial size of handaxe image is red and from condition with the smaller initial size of handaxe image.

Our second aim was to test the two predictions of the model. Figure 3.4 shows the empirically measured sizes, means, and variances of the chains over time, and their fit to the predicted values calculated according to the equations derived above. As $\text{Var}(S_g)$ depends on σ^2 , the empirically measured values of σ for each condition were substituted into the expression in order to calculate the predicted variances plotted in Figure 3.4B. As can be seen, the measured means do not seem to fit the predicted mean well, but the measured variances do seem to fit the predicted

variances. In order to formally test these hypotheses, we simulated the process described by the theoretical model, substituting in the empirically measured variances for each condition's distribution of copying errors, and matching the conditions of our experiment (i.e. 10 chains of 10 generations each in each condition). This was done with R (R Core Development Team, 2012) using code given in Appendix D. We derived empirical p-values by measuring the proportion of times that a value equal to or more extreme, in the appropriate direction, than the measured final mean and variance in each condition occurred over 10,000 simulations. For the larger-axe condition, the proportion of simulations where the final mean was equal to or more extreme than the empirically measured final mean was 0.01, and the proportion where the final variance was equal to or more extreme than the measured final variance was 0.44; for the smaller-axe condition, these values were 0.22 and 0.42 respectively. Thus, our visual intuitions are partly vindicated: the final mean in the larger-axe condition does deviate from the predicted mean more than expected by chance at the 5% significance level, but the final mean in the smaller-axe condition does not, while the final variances in both conditions do indeed not deviate from the predicted variances more than expected by chance at this significance level.

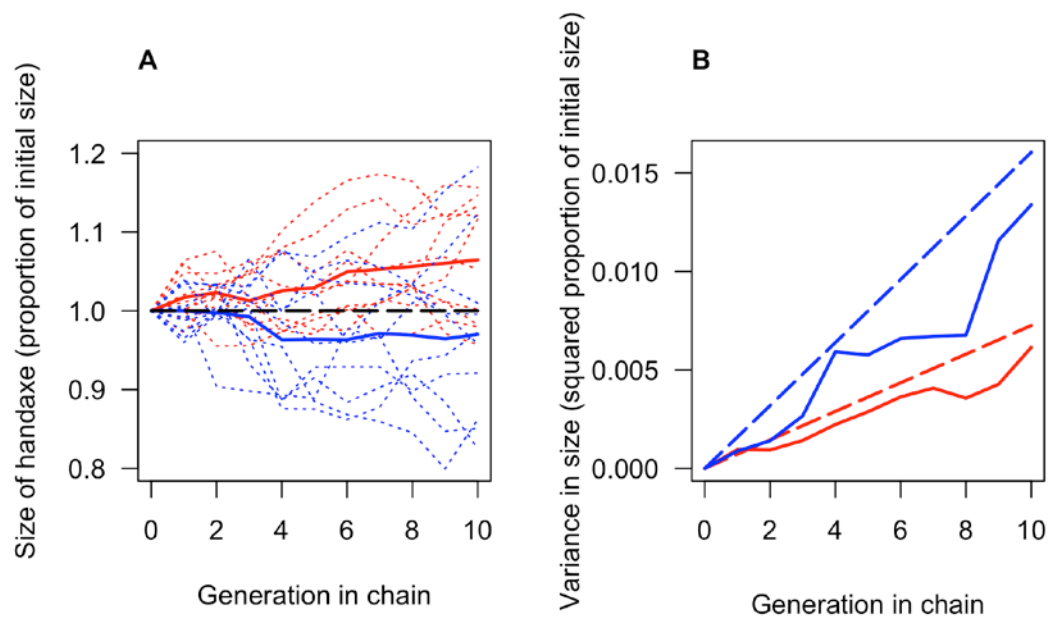


Figure 3.4. Results of the experiment compared to theoretical predictions. (A) Empirically measured sizes in each chain (thin dotted lines) and means across all chains in each condition (heavy solid lines) in both conditions. Data from the larger-axe condition is plotted in red and data from the smaller-axe condition in blue. The dashed black line shows the theoretically predicted mean. (B) Empirically measured variances across all chains in each condition (solid lines) and theoretically predicted variances (dashed lines) derived by using the empirically measured variance of the copying error distribution in each condition. Data and predictions from the larger-axe condition are plotted in red and from the smaller-axe condition in blue.

3.4. Discussion

The aim of this study was to provide the first explicit experimental test of the accumulated copying error model of cultural transmission, in which artifact variation increases due to imperceptible differences between a copy of an artifact and the original copied artifact. Acheulean handaxe images were transmitted along 20 independent chains each containing 10 participants, allowing us to measure inter-individual variation in copying error (σ^2) which has previously only been assumed from the psychophysics literature, in which transmission error and artifact evolution

are not the focus of study. We find that the ACE model gives good predictions of between-chain variance over time (see Figure 3.4B): in both the model and the experiment, between-chain variation increases exponentially over time as copying error causes different chains to diverge. Moreover, the empirically determined estimate of σ of 0.0343 resembles quite closely the copying error assumed in previous models of 3% (Eerkens & Lipo, 2005) which was derived from the psychophysics literature. This supports the use of this assumption in a cultural transmission context.

However, the empirical between-chain mean did not follow the predicted mean in the ‘larger’ condition, in which the initial size of the participants’ handaxe was larger than the target handaxe. It is also suggestive that in the ‘smaller’ condition, in which the participants’ handaxe started smaller, the measured between-chain means trended below the predicted mean, although the difference between the measured final mean and simulated final means was not significant at the 5% level. It will require more experimental testing to establish whether these biasing effects of the initial size of the object to be resized on its final size are not an artifact of using an iPad. If they are valid effects, they will have interesting implications for predicting ACE in archaeological data, as we would be led to expect that the size of artifacts created by ‘additive’ production methods (e.g. the weaving of baskets) as opposed to ‘reductive’ production processes (e.g. the manufacture of flaked stone tools) would evolve differently, with the size of additively-produced artifacts decreasing slowly through time and the size of the reductively-produced artifacts increasing, at least in instances where there is an effort to replicate faithfully the size of previously produced objects.

As the experiment shows that the model gives good predictions of between-chain variance, and we have estimated the shape parameter of the distribution of copying errors, we are now able to examine whether the model explains known data about the evolution of Acheulean handaxes. Happily, there exists a large database of morphological measurements on Acheulean handaxes, the Acheulean Biface Database (Marshall et al., 2002), against which we can test the model. The database includes length and breadth measurements for 2601 complete handaxes from 21 different sites in 5 countries (Morocco, South Africa, Tanzania, Israel, United Kingdom), with an age range of 1.5-0.3 million years ago. The coefficients of variation for length and breadth in this sample are 0.30 and 0.23, respectively. As deriving an expression for the coefficient of variation of all the artifacts created by a large number of independent chains over time is analytically difficult, we used simulations to estimate this quantity. The simulations were programmed in R using the general form $c_v(c$ (*replicate* (100, *cumprod* (*rnorm* (\mathbf{g} , 1, σ))))). Setting σ to our measured value of 0.0343, we find that the ACE model will generate c_v values greater than 0.30 in less than 200 generations, implying an obviously unrealistic lifespan of 4000 years for Acheulean handaxes (assuming a generation time of 20 years). Alternatively, we can set \mathbf{g} to 60,000, corresponding to 1.2 million years of evolution, the age range of the dataset, if each generation lasts 20 years, which shows that σ must be approximately 0.0017, or 20 times smaller than our measured value, in order to generate the measured c_v values. Since some of our participants wore eyeglasses, our measured value of σ probably errs towards being smaller than a typical ancient hominin value, which emphasizes the mismatch between our model and the data even further. Thus, as a general phenomenon, it is extremely unlikely that Acheulean handaxe size drifted as described by the ACE model.

Before fully accepting this conclusion, however, we should note some limitations of our analysis. First, the ACE model is potentially simplistic in its assumption that all of Acheulean evolution took place in independent lineages; incorporating empirical data on the amount of branching that occurred into the model may allow it to make more realistic predictions. Second, although large, the comparative handaxe dataset used here is not exhaustive in terms of regional or temporal coverage and provides only a broad guide to how Acheulean handaxe size variation compares to the ACE model. While our data suggest that at its broadest scale Acheulean handaxe size variation does not conform to the ACE model, this does not rule out more localized instances of such drift. Indeed, regionally-specific trends of temporal change in handaxe size have been suggested previously (e.g. Gilead, 1970; Baskaran, 1986; Rajaguru, 1985), including geographically-localised instances of cultural drift that represent deviations from wider patterns due to situationally-specific circumstances (e.g. in India: Lycett & Bae, 2010). Recent analyses have emphasized how spatial and temporal factors might affect cultural patterning under neutral conditions (e.g. Lycett & von Cramon-Taubadel, 2008; Hamilton & Buchanan, 2009; Premo, 2012; Pérez-Losada & Fort, 2011). Given these factors, an important future extension of this study may therefore be to incorporate more explicit geographical parameters into the copying error model (e.g. spatial factors) and compare these revised models against artefactual data with high temporal and spatial resolution.

Assuming that Acheulean handaxe size *does* broadly deviate from the ACE model, we see three possible explanations for this deviation. Firstly, concepts of appropriate limits for handaxe size may have been stabilised by functionally-related cultural

selection: for example, by the need to fit into tool users' hands, a highly plausible selective pressure (Crompton & Gowlett, 1993; Gowlett, 2006). Secondly, handaxe size may have drifted in a way that stabilized variation: some models of this for quantitative traits were given by Cavalli-Sforza and Feldman (1981). A third explanation for the suggested deviation from the ACE model might be due to the possibility that firm concepts of handaxe *size* (opposed to handaxe production methods leading to their essential and distinctive *shape* properties) may not strictly have been socially transmitted at all. An alternative possibility here is that as functional handheld tools, individuals gained an intuitive sense of what a 'good sized' handaxe was via their own empirical engagement with material properties and their various outcomes during usage. This idea resembles a hypothesis proposed by Tennie & Hedwig (2009), who noted that some traits in great ape cultural traditions might have been fostered by stimulus enhancement of the trait's raw materials. This may also mean that (somewhat like shoes or other items of clothing) what is an 'optimally-sized' handaxe may vary somewhat from individual to individual depending on their own physical size, strength, etc., in turn leading to patterns of variation in handaxe size that deviate from the ACE model. We note, however, that within any socially-mediated context of observation and learning about handaxe production and usage, some notion of suitable size parameters is also likely to have been inducted in novice handaxe producers. Of course, some combination of these causes is also possible. Each of these explanations suggests a number of promising directions for further research.

In conclusion, we have provided a theoretical reformulation and novel experimental test of the ACE model of cultural mutation, in which artifacts change purely due to

imperceptible differences between a copied artifact and the original, and which has been proposed as a null model for the cultural evolution of artifacts in the material record. Our experimental test supports the prediction that ACE causes artifact size variation to increase exponentially. However, it did not fully support the prediction that mean artifact size should remain unchanged, instead finding that the initial size of the to-be-copied artifact may bias the eventual copied artifact size. This suggests that the ACE model needs to be revised to incorporate this priming or biasing effect, and that future empirical work might seek to test this effect by comparing reductive and additive technologies. Finally, having established experimentally the validity of the ACE prediction concerning artifact size variation, we apply this prediction to an actual empirical dataset, showing that Acheulean handaxes do not fit the expectation of the ACE model, and we suggest potential alternative explanations for this deviation.

Chapter 4.

Cultural differences and cumulative culture: parameterizing the differences between human and nonhuman culture

This chapter was co-authored with Stephen J. Lycett and Alex Mesoudi. It is currently being prepared for submission to *Journal of Theoretical Biology*.

Abstract:

Diverse species exhibit population-specific profiles of socially learned traits, from songbird dialects to primate tool-use behaviours. However, only humans appear to possess cumulative culture, in which cultural traits increase in complexity over successive generations. Theoretically, it is currently unclear how cognitive and demographic factors give rise to these phenomena, and how to explain the difference between cumulative and non-cumulative cultural regimes. Here, we address this by constructing and analysing cultural evolutionary models of both phenomena that replicate empirically attestable levels of cultural variation and complexity in chimpanzees and humans. In our model of cultural differences, we find that realistic cultural variation between populations can be maintained even when individuals in different populations invent the same traits and migration between populations is frequent. Our model of cumulative culture indicates that both the accuracy of social learning and the number of cultural models interact to determine the complexity of a trait that can be maintained in a population. Combining these models creates two qualitatively distinct regimes, determined by the interaction of cognitive and demographic factors, in which there are either a few, simple traits, or many, complex traits, and suggest that these regimes correspond to the type of phenomena represented by nonhuman and human cultures, respectively.

4.1. Introduction

Many animal species can learn socially (Galef and Laland 2005); examples include the transmission of food preferences in rats, shoaling routes and nest site locations in fish, and foraging locations in bees and ants (Helfman and Schultz 1984; Laland and Plotkin 1990; Leadbeater and Chittka 2007). Some of these species show cultural differences in the ‘trait-profiles’ of different populations, such as differences in the song dialects of different bird populations and in the presence or absence of various behaviours in different populations of chimpanzees and orangutans (Catchpole and Slater 2003; van Schaik et al. 2003; Whiten et al. 1999). Only humans unambiguously appear to also have cumulative culture (though there are possible reports in chimpanzees: Boesch et al. 2009), meaning cultural traits that depend on other traits (Boyd and Richerson 1996; Enquist et al. 2011; Tomasello et al. 1993); examples abound in technology, science, and mathematics (Basalla 1989; Hodgkin 2005; Longair 2003). One typical feature of cumulative culture is that traits become more complex than an individual could invent within their lifetime, because the trait has accumulated over successive generations (Boyd and Richerson 1996).

Here we analyse models of both cultural differences and cumulative culture, and ask what causes the difference between human and nonhuman culture. There has been much work modelling the biological evolution of the capacity for social learning and culture, including various cultural transmission biases (Boyd and Richerson 1985; Kendal et al. 2009a; Rogers 1988; Wakano et al. 2004). We are interested in a different, related question: how do the dynamics of cultural (micro)evolution, caused by biologically-evolved cognitive capacities and social structures, lead to the phenomena of cultural differences and cumulative culture? While some models *have*

addressed this question, none suitably answer it in its broadest sense. Previous models of cultural differences have posited that different cultural traits are optimal in different ecologies and asked how cultural evolution can create and maintain cultural differences (Boyd and Richerson 1985; Henrich and Boyd 1998). However, previous demonstrations of cultural differences in non-human species explicitly attempted to exclude behavioural variation attributable to ecological differences (van Schaik et al. 2003; Whiten et al. 1999), raising the question of how cultural differences may arise purely due to the dynamics of cultural evolution. Previous models of cumulative culture have either not posited a strict dependence of more complex traits on simpler traits (Henrich 2004; Kobayashi and Aoki 2012; Mesoudi 2011b; Powell et al. 2009), have been specific to one or two species (Mesoudi 2011b; Pradhan et al. 2012), or have modeled culture at the population rather than the individual level (Enquist et al. 2011). We are interested in understanding the question of how cumulative culture arises at the level of the individual, and in a species-general manner.

In order to answer these questions, we build on previous models by Strimling et al (2009b) and Enquist et al (2010), which are elegant, simple, and tractable. Using these previous models as a basis for our own provides direct continuity with past work on this topic and ensures that we begin from a rigorous starting point; yet we also go beyond these existing models to address novel questions concerning cultural differences and cumulative culture. In Strimling et al's model, individuals are born, learn some of the cultural traits known by another individual, possibly invent new cultural traits, and eventually die. Traits are independent of each other, have identical cultural fitness, and have no effect on biological fitness. These are simplifying assumptions, probably unrealistic for some traits (e.g. foraging behaviours), but

possibly good approximations for many others (e.g. social customs or self-medication behaviours). Strimling et al showed how the number of different traits found in the population and the number of traits known by each individual increased as a function of population size, individuals' social learning accuracy, and individuals' innovativeness.

Enquist et al (2010) showed that stable cultural traditions could never emerge if a trait is learnt from a single cultural model (e.g. one biological parent), assuming that the accuracy of social learning is not perfect. They further showed that neither independent invention, multiple learning trials, nor biological fitness benefits change this result significantly. They then showed that learning from multiple cultural models allows stable traditions to emerge, and derived the stable population frequency of a trait as a function of the accuracy of social learning and the number of cultural models.

We extend these models to analyse cultural differences and cumulative culture. To Strimling et al's model we add multiple populations that interact through migration, allowing a comparison of different populations' trait profiles. To Enquist et al's we add a linear succession of complexity levels to the trait, simulating the accumulation of cultural knowledge over successive generations. Finally, we combine these models and ask what features cause the appearance of these two different phenomena.

4.2. Cultural differences

Strimling et al's (2009b) model contains three stages. First, one of the N individuals in the population is picked at random, dies, and is replaced by a naïve individual.

Second, the naive individual picks one other individual at random and independently learns every trait that individual knows with probability a per trait ($0 < a < 1$).

Third, the individual invents a random number of new traits with expectation μ . To this we add a fourth stage, in which the individual migrates to another population with probability $\frac{m}{2}$ ($0 \leq m \leq 2$). There are p such populations in the metapopulation, and the individual is equally likely to migrate to any of them. When the individual migrates, it swaps population memberships with a randomly chosen member of its target population, so that the size of each population remains constant. Because each migration event involves two individuals and the target population is picked at random, the expected number of individuals who migrate away from any given population in one timestep is $\frac{m}{2} + \frac{\frac{m}{2}(p-1)}{p-1} = m$; this is why m is halved above. Since individuals can only migrate if they were ‘born’ in the current generation, this corresponds to ‘young’ individuals migrating.

In order to model multiple populations of such learners, we must also decide which traits individuals invent. Strimling et al do not specify this, assuming only that individuals always invent traits that are currently unknown in the population.

Lehmann et al (2011), using a similar model, assume that there are a very large number of traits, tending towards infinity, and individuals invent a random trait chosen from this set. However, clearly, a number of different populations in which individuals know only a small number of traits which were invented by picking at random from a very large set will tend to be completely dissimilar in the composition of their trait-profiles, and strikes us as unrealistic. Thus, we assume instead that there are infinitely many traits which are invented in a fixed sequence that is the same in all populations. We use the simplest possible sequence, in which traits are labeled by the

natural numbers and invented in the order 1, 2, 3, etc. Individuals always invent the first trait in the sequence that is not currently known by any individual in their population. This represents an idealized situation in which individuals' physical and cognitive predispositions and the nature of their physical and social environments create a clear ranking in the 'obviousness' of traits; for example, technologies for foraging easily-visible food resources may be invented before technologies for foraging hard-to-find foods, and foraging technologies in general may be invented before social or symbolic behaviours that are less important for survival. While this situation is clearly idealized, it is more realistic than assuming random draws from a large set of traits, and it is simple enough to analyse. Note that these traits are not cumulative; later traits do not build on earlier traits, and an individual can socially learn any set of traits irrespective of the traits' position in the sequence. A trait may also be lost from the population and later re-invented without affecting any other traits.

Fig. 4.1 shows the time course and end result of one simulation of the model. (A graphic illustrating an end result of the model is available in Appendix E, Figure E1.) Fig. 4.1a shows that the number of different traits known in each population, called S by Strimling et al, hovers around the expected value they derived. Fig. 4.1b shows the trait-profiles present in each population at the end of the simulation. Intuitively, one expects that if all populations invent the same traits in the same order, different populations will have identical trait profiles. However, the trait-profiles in Fig. 4.1b clearly show variation between populations. To quantify this variation we define s , the cultural similarity between two populations, in the same way as Enquist et al (2011):

$s = \frac{|X \cap Y|}{|X \cup Y|}$, where X is the set of traits known in the first population and Y is the set

known in the second. Thus, s is the proportion of all traits known in either population that are known in both populations. To compare more than two populations we define \bar{s} to be the mean similarity between every possible combination of populations in a metapopulation.

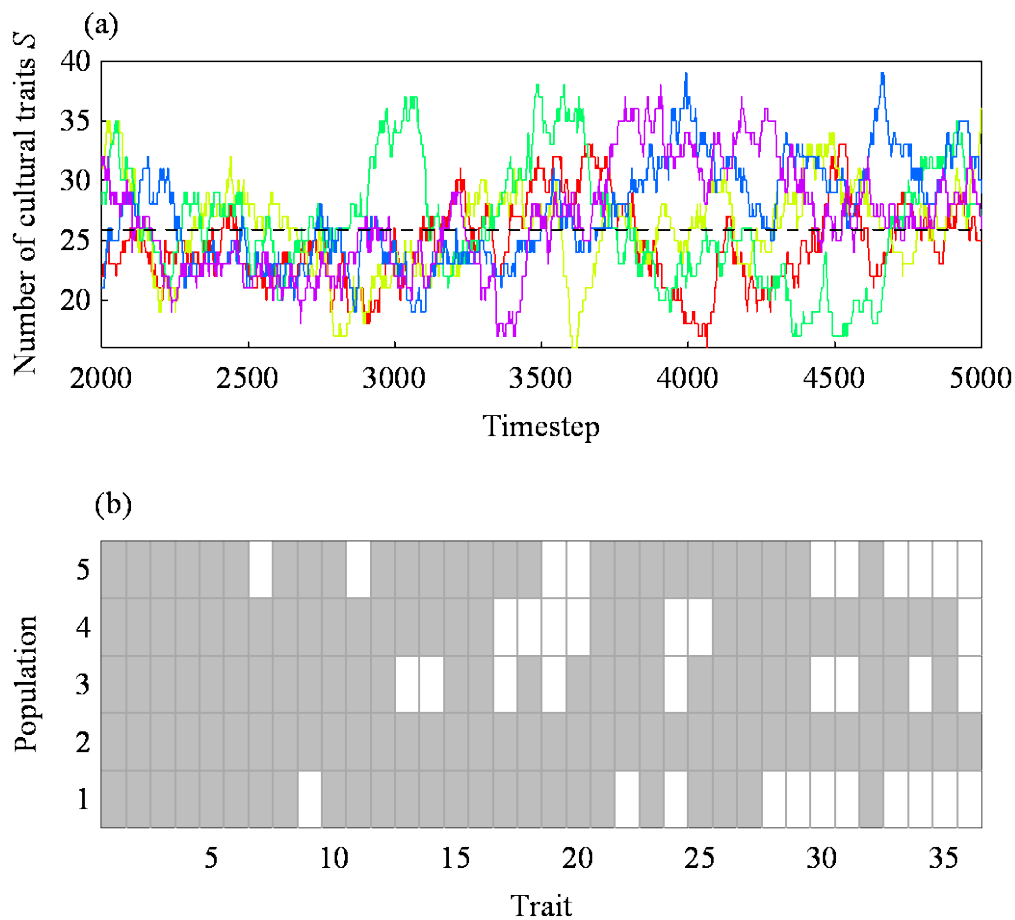


Figure 4.1. One simulation of the cultural differences model. (a) Time series of the number of traits S known in each population. The initial part of the simulation is not shown. The dashed line shows the exact expected value derived by Strimling et al (2009b). (b) Trait-profiles of each population at the end of the simulation, with grey cells marking the presence of a given trait in a given population and white cells marking its absence. The average similarity \bar{s} between the populations is 0.71. Parameter values: $N = 100$, $a = 0.9$, $\mu = 0.1$, $m = 0$, $p = 5$.

Fig. 4.2 shows how the mean similarity between populations \bar{s} increases with population size N (in a decelerating way) and accuracy of social learning a (in an accelerating way). Fig. 4.2c shows how \bar{s} varies across the parameter space created by N and a , demonstrating that no realistic parameter values generate complete inter-population homogeneity. The reason that the assumption of a fixed sequence of traits does not lead to complete population homogeneity is trait loss. Since Enquist et al's model (2010), in which individuals learn from one cultural model, is in effect contained within Strimling et al's model, it is clear that traits must eventually be lost because of imperfect social learning. We show in Appendix F that in the absence of migration, the probability that a trait will spread beyond its inventor is

$$\frac{a}{1+a}.$$

Since a must be less than 1, this probability is always less than $1/2$. In other words, most newly invented traits die out with their inventor, even with high fidelity cultural transmission. This feature of the model accords reasonably with evidence on chimpanzee (*P. t. schweinfurhii*) inventions documented at Mahale, Tanzania, where approximately 43% of innovations documented over a 30-year period did not spread socially (Nishida et al. 2009). In the model, this frequent loss of traits is balanced by the re-invention of traits that have been lost, and this dynamic creates the moderate dissimilarity between population trait-profiles.

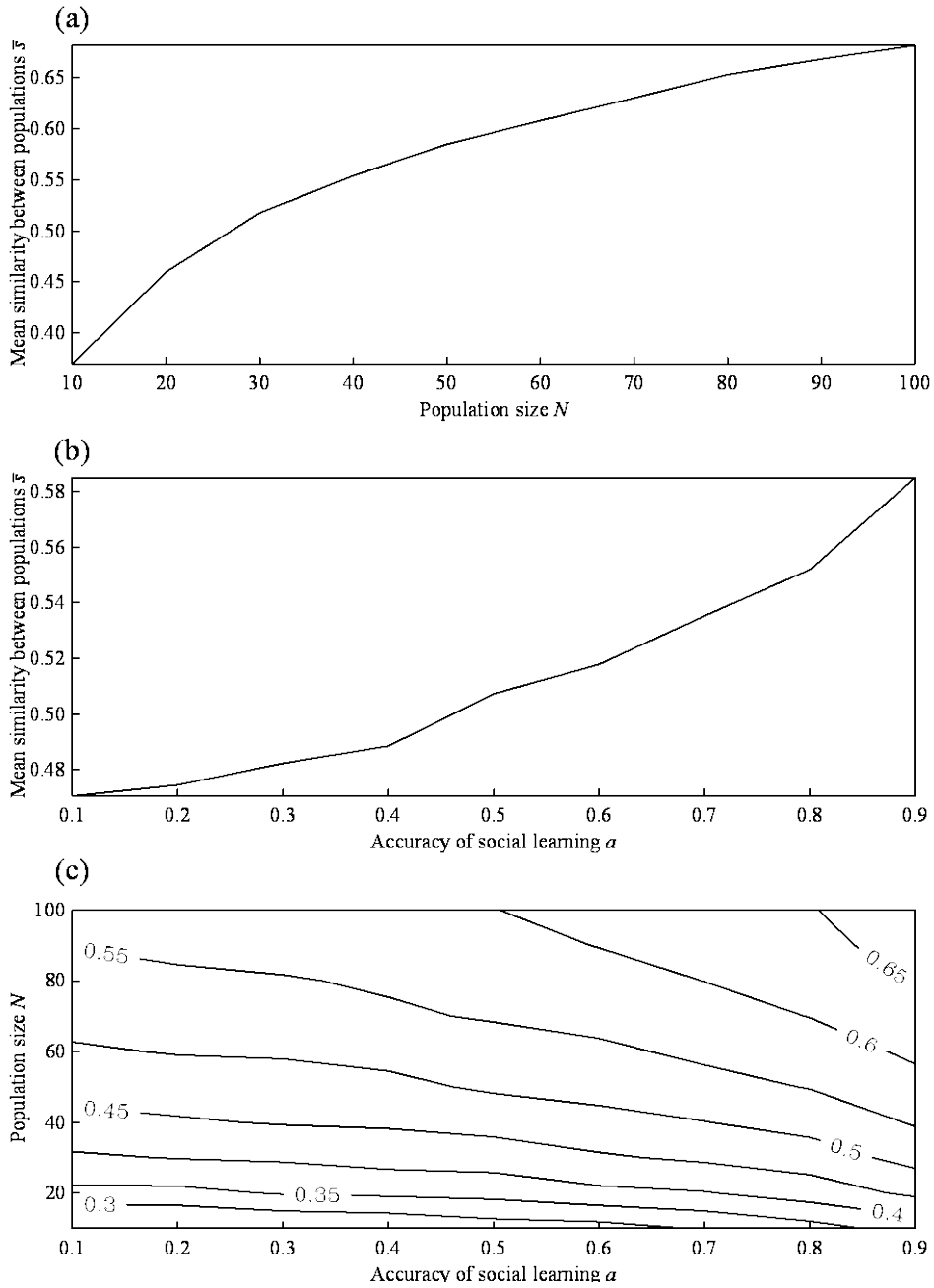


Figure 4.2. The effect of (a) the population size N , (b) the accuracy of social learning a , and (c) both, on the mean similarity between populations \bar{s} . Panel (c) shows the value of \bar{s} on a contour plot in an analogous way to a geographical map showing the height of a mountain at various points in space. All panels show the value found after 2000 timesteps, averaged over 1500 simulations with parameter values $\mu = 0.1$, $p = 5$, and $m = 0$; in (a) $a = 0.9$ and in (b) $N = 50$.

We now analyse the effects of migration. Fig. 4.3 shows how the mean number of different traits known in a population \bar{S} and the mean similarity between populations \bar{s} increase with m . We show values from simulations with m ranging from 0 (no migration) to 0.5 (half of all individuals migrate); the latter may be realistic in both human bands (Hill et al. 2011), and in chimpanzees, where one sex disperses. As expected, migration makes populations more similar in their trait-profiles, but even frequent migration does not completely homogenize them. Migration also increases the total number of traits known, because migrants can bring traits that have not been invented in the target population; this resembles the effect found by (Powell et al. 2009), but not as pronounced. A possible empirical example of this is the introduction of ant-fishing into the Kasekela chimpanzee (*P. t. schweinfurthii*) community by a female immigrant from the Mitumba community (Gombe NP, Tanzania: O'Malley et al 2012). However, this is likely only to occur in specific circumstances, such as when the migrants are relatively older individuals and are thus preferred over younger individuals as cultural models (Biro et al., 2003).

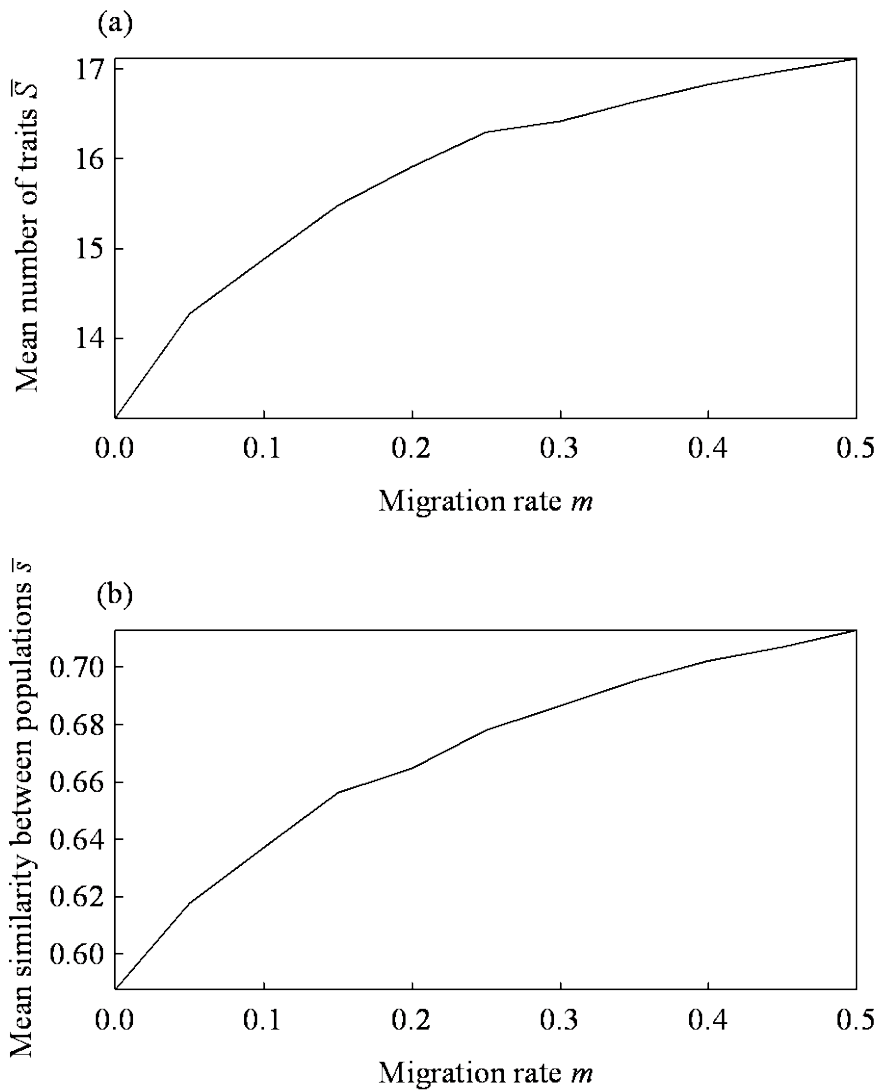


Figure 4.3. The effect of the migration rate m on (a) the mean number of different traits across all populations \bar{S} and (b) the mean similarity between populations \bar{s} . Both panels show the value found after 2000 timesteps, averaged over 2000 simulations with parameter values $N = 50$, $a = 0.9$, $\mu = 0.1$, and $p = 5$.

To compare the results shown in Fig. 4.3b with empirical data, we calculated the values of \bar{s} from data reported on chimpanzees (*Pan troglodytes*) (Whiten et al. 1999) and orangutans (*Pongo pygmaeus*) (van Schaik et al. 2003), ignoring all comparisons involving traits thought to be absent for ecological reasons or insufficient observation. The values of \bar{s} were approximately 0.46 and 0.32, respectively. Note that these

values probably underestimate the true values, because these studies only included traits that the investigators suspected *a priori* might vary between populations. With this in mind, Figs. 4.2c and 4.3 show that the model produces realistic between-population variability.

4.3. Cumulative culture

Enquist et al's (2010) model tracked the dynamics of a single cultural trait in a population. The model has two parameters, which we rename for consistency with Strimling et al's model: a , the accuracy of social learning, and n , the number of cultural models. As above, both parameters are assumed to be constant across all individuals. We extend their model in the following way. The population consists of N individuals, and as above, in each time step a randomly chosen individual dies and is replaced by a naive individual. The individual then randomly picks n other individuals from the population to be its cultural models. The individual attempts to learn the trait from each of the n models in turn. Whether this learning is successful depends on whether or not the models carry the trait and on a . Finally, the individual innovates with probability μ .

The trait has an infinite number of complexity levels. Learning any given level is dependent on having learnt all previous levels. The levels represent cumulative improvements that can be made to the basic, level 1 trait. Thus, they may roughly correspond to Oswalt's (1976) 'techno-units', or to successive modifications to a technology or social practice; plausible definitions and examples of different levels are given by Pradhan et al (2012). In our model, individuals learn these levels as follows: for each cultural model, the individual learns the first level of the trait that it

does not already know with probability a , and moves on to the next level if successful, which it again learns with probability a , and so on. Thus the probability of a naive individual learning a given level l from a model who knows at least l levels of the trait is a^l . After social learning, each individual has a probability μ of improving its knowledge of the trait by one level through innovation.

Thus, in our model ‘cumulative culture’ is implemented as a strictly ‘ladder-like’, hierarchical process, as opposed to the more ‘fluid’ implementation in previous models such as that of Henrich (2004), in which individuals can jump from any level of a trait to any other. To our knowledge our model is the first general model of cumulative culture using ‘ladder-like’ traits. Additionally, innovation in our model takes place at the individual level, rather than the population level, allowing us to observe the growth of cumulative culture at the population level as a macroevolutionary process created by microevolutionary individual innovation events.

We are interested in understanding how \bar{l} , the mean level that a population maintains, depends on the accuracy of social learning a , the number of cultural models n , and the innovativeness μ . In each simulation of the model the population begins completely unknowledgeable. Fig. 4.4 shows the time course and end result of one simulation of the model. (A graphic illustrating a time course of the model is available in Appendix E, Figure E2.) In Fig. 4.4a we see that the mean level of the trait in the population initially rises and then stabilizes; Fig. 4.4b shows the resulting distribution of levels amongst the individuals of the population.

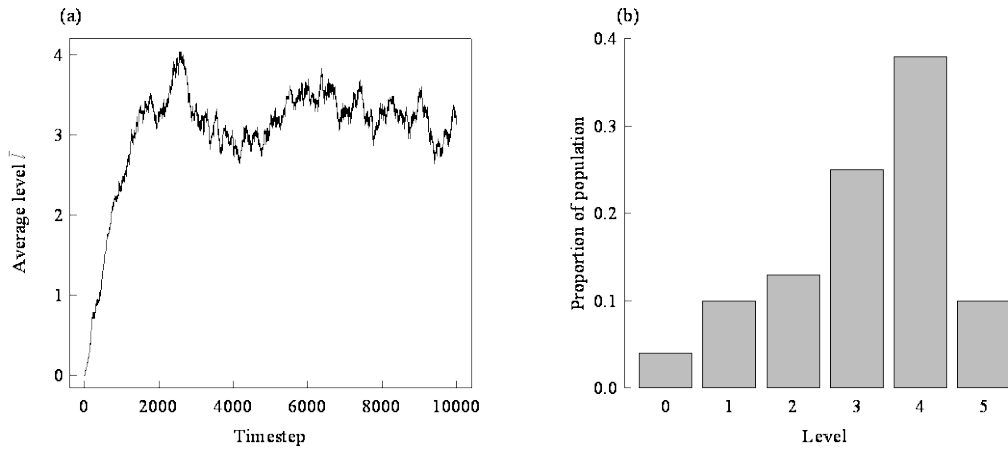


Figure 4.4. One simulation of the cumulative culture model. (a) Time series of the mean level \bar{l} known in the population. (b) The distribution of levels in the population at the end of the simulation. Parameter values: $N = 100$, $a = 0.7$, $n = 3$, $\mu = 0.1$.

Fig. 4.5 shows the effects of a and n on the mean level \bar{l} of the trait that is maintained in the population. The mean level \bar{l} increases linearly with n (Fig. 4.5a), and non-linearly with a (Fig. 4.5b). When varying the innovativeness μ in simulations, we found that increasing μ from 0.1 to 1 increases \bar{l} by ≈ 3 regardless of the values of the other parameters; thus, the effects of a and n are much stronger than the effect of μ . Fig. 4.5c shows how \bar{l} varies across the parameter space created by a and n . Enquist et al showed that only if $an > 1$ could the trait be stably maintained in the population through social learning in their model. Since the trait in their model corresponds to the basic level 1 trait of ours, this result clearly applies here too. Much of the parameter space features realistic levels of accumulation; compare the values of \bar{l} shown in Fig. 4.5c to the mean techno-unit values of 3-7 found by an empirical analysis of the complexity of marine foraging technology in a number of Oceanic human populations (Kline and Boyd 2010). However, there are clearly many different combinations of a and n that will maintain a given mean level \bar{l} in the population; thus, observing a

given level of accumulation in a population does not allow us to completely identify the values of a and n for that population. Note that in the simulations shown in Figs. 4.4 and 4.5 the population size $N = 100$, as opposed to $N = 50$ in the simulations shown in Figs. 4.2 and 4.3, corresponding to the increase in the effective population size among later hominin species and *Homo sapiens* compared to non-human great apes.

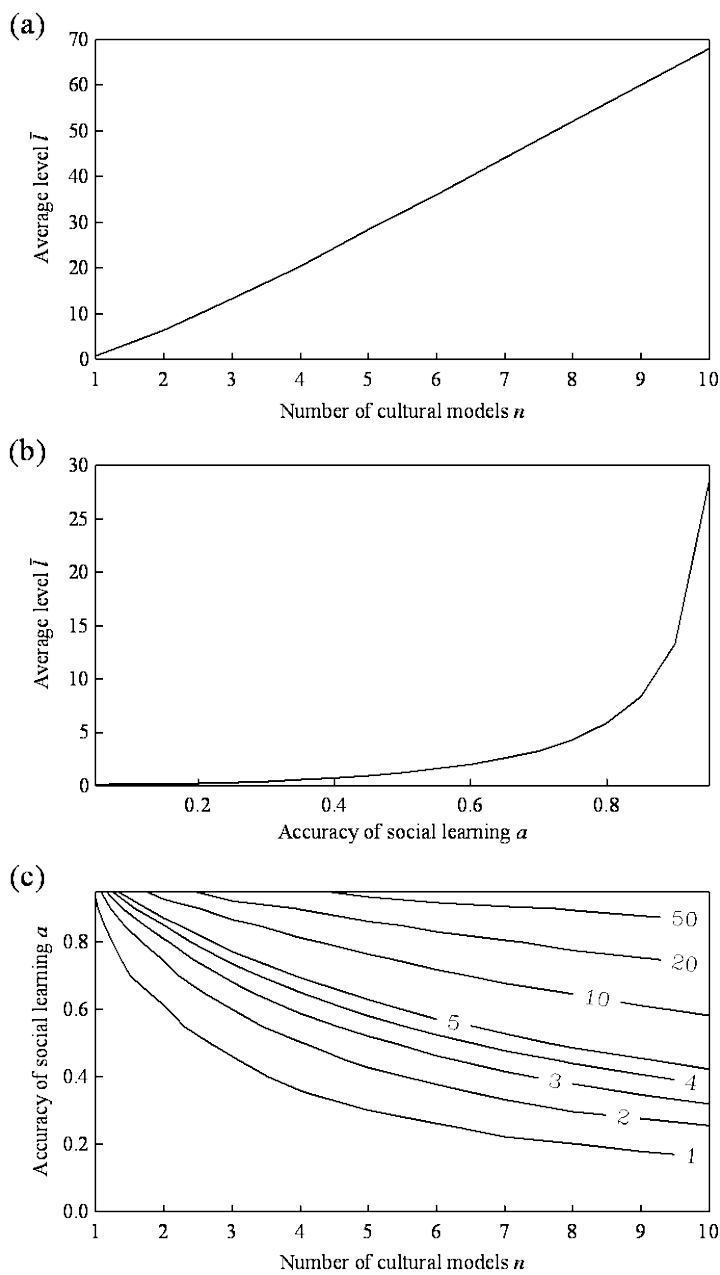


Figure 4.5. The effect of (a) the number of cultural models n , (b) the accuracy of social learning a , and (c) both, on the mean trait level \bar{l} maintained in the population. All panels show the value found after 10000 timesteps, averaged over 20 simulations, with $N = 100$ and $\mu = 0.1$; in (a) $a = 0.9$ and in (b) $n = 3$.

4.4 Combined model

we note that our two models can be combined. Imagine that each trait in the first model comes in the infinite number of levels described in the second model, and that instead of choosing only one cultural model, naive individuals choose n cultural models, learn from them, and then both invent new traits and improve existing ones. The structure of the traits and trait levels in this model is shown in Fig. 4.6. As shown in the figure, the difference between traits and trait levels corresponds to the distinction drawn by Dean et al. (2013) between cultural ‘accumulation’ and ‘cumulative culture’: in the first, it is the number of cultural traits that increases, and in the second their quality. The combined model then simulates the dynamics of independent cumulative traits within and between populations that interact by migration. To fully analyse the model, a choice must be made as to how individuals innovate cumulative traits; whether, for example, there is a fixed expected number of improvements per individual, or whether more knowledgeable individuals make on average more improvements. Unfortunately there is little empirical evidence on this question.

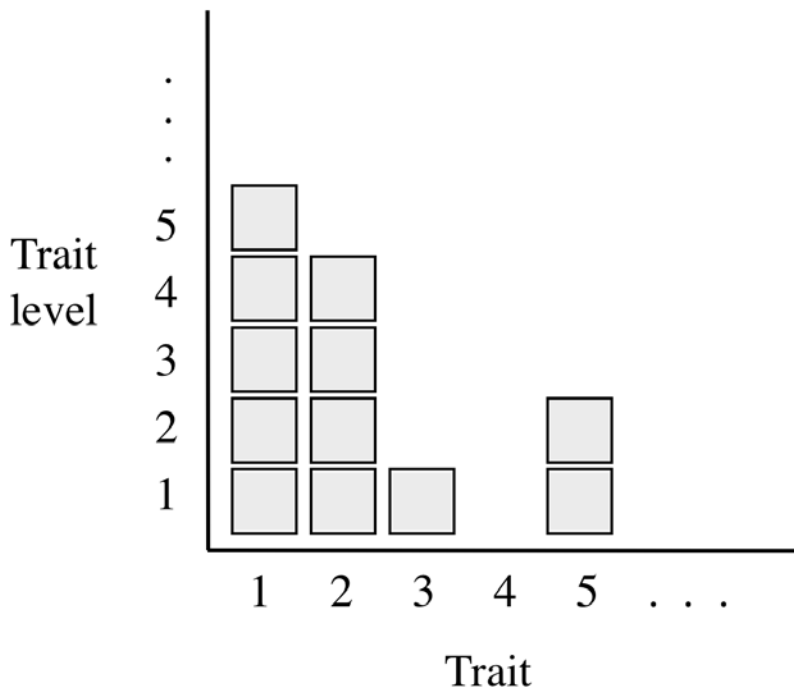


Figure 4.6. A schematic illustration of the structure of the traits and trait levels for one hypothetical individual in the combined model. In this example, the individual knows trait number 1 to level 5, trait number 2 to level 4, trait number 3 only at the first level, does not know trait number 4, and knows trait number 5 to level 2.

Without deciding this one way or another, we can still make useful statements about the combined model. Consider the expected number of different traits S in a population. If $n = 1$, Strimling et al (2009b) derived an analytical approximation for S , which shows that, for realistic but high values of these parameters, say $N = 100$, $a = 0.9$, and $\mu = 0.5$, $S \approx 133$ traits. On the other hand, if $n > 1$, no analytical approximation for S is known, but we can approximate S by following Strimling et al and noting that $S = \mu NT$, where T is the expected lifetime, in generations, of a newly invented trait. We conducted simulations that showed that even for very small values of the parameters which satisfy the criterion $an > 1$, say $N = 30$, $a = 0.65$, and $n = 2$, $T \approx 100$, and that T increases very rapidly with increases in the parameters.

Assuming additionally a low value for innovativeness, e.g. $\mu = 0.1$, $S \approx 300$ traits (a simulation showing this is given in Appendix E, Figure E3) and rises very quickly into the thousands and tens of thousands of traits with increases in the parameters. Moreover, the condition $an > 1$ is also the condition for cumulative culture to arise, as noted above.

4.5. Discussion

Our models give results that mimic the phenomena of between-population cultural differences and cumulative culture in reasonably realistic ways. In our model of cultural differences we find that realistic differences between populations are maintained despite assuming that all individuals invent the same traits in the same order, and despite frequent migration between populations. This occurs because traits die out with non-negligible frequency, and most traits do not spread beyond their inventor. In our model of cumulative culture, we find that the accuracy of social learning, a cognitive factor, and the number of cultural models, a demographic factor, interact to determine the cumulative level of a trait that a population can stably maintain, and that large portions of the parameter space feature realistic levels of accumulation.

Our first result implies that cultural differences between animal populations do not necessarily reflect ecological or genetic differences, which has been a matter of some debate (Laland and Galef 2009). Moreover, it is clear from our results that cultural differences between animal populations also need not be caused by model biases or conformity within differing populations. Furthermore, the time series in Fig. 4.1a imply that phenomena such as chimpanzee cultures have inherent historical

dimensions (Lycett 2010), which have indeed begun to be investigated using archaeological (Haslam et al. 2009) and phylogenetic (Lycett et al. 2007) methods. Our second result implies that neither cognitive nor demographic factors are the sole explanation for the evolution of cumulative culture, which again has been the topic of some discussion (Powell et al. 2009). The dependence of cumulative culture on two different factors may help to explain its rarity in nature. Moreover, the strong influence of these two factors and the weak influence of innovativeness per se on cumulative culture may cast doubt on the ‘cognitive niche’ explanation of hominin success put forward by Pinker (2010), in which rapid innovation is key. The model instead lends support to the ‘cultural niche’ interpretation of Boyd et al. (2011), in which cumulative culture is the main driving force behind successful hominin adaptation to changing and varied environmental conditions.

Finally, we note that our analysis of the combined model shows that the model has two qualitative regimes, with the threshold created by the interaction of both cognitive and demographic factors. When $an < 1$, the number of traits known in the population is relatively low and there is no cumulative culture. When $an > 1$, many traits are known in the population and there can be cumulative culture. We suggest that these regimes correspond qualitatively to nonhuman and human cultures, respectively.

Chapter 5.

The 'fundamental theorem of cultural selection'

Under review at *Biology and Philosophy*.

Abstract:

R. A. Fisher's 'Fundamental Theorem of Natural Selection' gave a mathematical basis to the theory of biological evolution by natural selection. In this chapter, I give a new interpretation to an existing mathematical theorem called the growth-rate theorem, allowing it to be understood as the 'fundamental theorem of cultural selection'. I explain the meaning of this theorem and argue that it fulfills a similar function to Fisher's Theorem, providing a mathematical basis for the theory of cultural evolution by cultural selection. I also argue that it can give conceptual clarity to, and shed light on, the concept of cultural selection and the processes of cultural evolution.

5.1. Introduction

In 1930, R. A. Fisher gave what he called 'The Fundamental Theorem of Natural Selection' (Fisher, 1930). His purpose in doing so was, in his words, to "state the principle of Natural Selection in the form of a rigorous mathematical theorem, by which the rate of improvement of any species of organisms in relation to its environment is determined by its present condition" (ibid, p.22). The aim of this chapter is to give a similar theorem for the theory of cultural evolution. Specifically, I propose that a similar 'fundamental theorem of cultural selection' can be found by giving a new, cultural interpretation of an existing mathematical theorem called the growth-rate theorem.

The structure of the chapter is as follows. In section 2, I summarise the meaning, history, and usefulness of Fisher's Fundamental Theorem. In section 3, I summarise the theory of cultural evolution, present the 'fundamental theorem of cultural selection', and explain its interpretation and usefulness. Finally, in section 4, I conclude and discuss the connection between the theorem and Price's equation.

5.2. Fisher's Fundamental Theorem

Fisher's Fundamental Theorem of Natural Selection was given in Chapter II of his 1930 book *The Genetical Theory of Natural Selection* (Fisher, 1930). Fisher stated the Theorem as follows: "*The rate of fitness of any organism at any time is equal to its genetic variance in fitness at that time.*" (ibid, p.35; italics his). His verbal statement is somewhat cryptic and the Theorem is easier to understand in the paraphrased words of Edwards (1994, p.450): "The rate of increase in the mean fitness of any organism at any time ascribable to natural selection acting through changes in gene frequencies is

exactly equal to its genic variance in fitness at that time". A mathematical statement may also be given using the notation of Edwards (1994): $\Delta w = v$, where w is the normalized mean fitness and v is the variance in that fitness.

Before describing the Theorem in more detail, it is worth saying a little about the history of the reception of the Theorem. From its publication in 1930 until 1972, it was either ignored or misunderstood by geneticists, who (partly because of Fisher's unclear wording) thought that the Theorem referred to the total change in mean fitness rather than the partial change in mean fitness due to natural selection. In 1972 G. R. Price wrote a paper arguing that the true meaning of the Theorem had been misunderstood (Price, 1972), and since then it has been discussed by Edwards (1994; 2002), Ewens (1989; 1992; 2011), Frank & Slatkin (1992), Lessard (1997), and Okasha (2008), among others. My description of it that follows is heavily indebted to these authors.

The essence of the Theorem is to identify the equality between the rate of change of the mean fitness of a population and the 'genic', or additive genetic, variance in fitness amongst individuals in that population. The Theorem rapidly became famous because it implied that mean fitness always increases (because a variance is never negative). However, the Theorem is only concerned with that part of the total change in mean fitness that is "ascribable to natural selection acting through changes in gene frequencies" (from the above quote from Edwards, 1994). In addition to natural selection, a number of other factors will interact to determine the mean fitness of a population at a given time: mutation, migration, drift, and environmental change (both of the natural and social environments), as well as the effects of genetic combinations

through epistasis and dominance. The Theorem is not concerned with any of these factors and instead only quantifies the increase in mean fitness due to natural selection that *would* take place if every gene in the population were to retain the same fitness after selection as it had before selection.

While mutation, migration, drift, and environmental change are commonly thought to be separate evolutionary factors from natural selection, the fact that the Theorem does not take account of genetic effects like dominance and epistasis may seem strange, as these are commonly thought to be integral parts of the action of selection. However, in Fisher's derivation the Theorem is based on the average effect of each gene, and it must be understood from the gene's 'point of view', which was later to be influentially propounded by Dawkins (1976). From the metaphorical point of view of a particular gene (strictly speaking, allele), the other genes (alleles) present in 'its' genome are part of the environment it finds itself in. Thus the effects of dominance and epistasis constitute part of what can be called the 'genetic environment', and can be partitioned from the effect of natural selection on the frequencies of genes (alleles).

It is important to understand that, since it does not incorporate the effects of mutation, migration, drift, or changes in the natural, social, or genetic environment, the Theorem is not useful for predicting evolution; in almost all circumstances, these factors will have important effects on mean fitness. Rather, it quantifies the extent to which the population, viewed as a population of genes, becomes adapted by natural selection to the environment it was previously in. Moreover, organisms tend to be highly adapted to their environments and have relatively stable population sizes, and Fisher expressed the view that "for the majority of organisms, therefore, the physical

environment may be regarded as constantly deteriorating" (Fisher, 1930, p.41). This deterioration of the environment, along with the effects of the other factors not included, generally counterbalances the adaptive, fitness-increasing effect of natural selection.

What, then, is the value of Fisher's Theorem? It is a clear mathematical statement of how evolution by natural selection brings about adaptedness. Though of little practical value, it has great conceptual value, because it formalises the workings of natural selection.

An example of its conceptual value is given by Frank & Slatkin (1992). In birds, higher clutch sizes frequently increase fitness, and birds have intraspecies variation for clutch size, yet often clutch sizes remain stable over time (Cooke et al., 1990). They suggest that the partition of total fitness change into fitness change caused by natural selection and fitness change caused by the change of the environment, which arises naturally from Fisher's Theorem, can explain the stability of total fitness, because selection for increased clutch size is exactly counterbalanced by increased competition from other birds in the population. They also argue that Fisher's Theorem may explain many other similar 'Red Queen'-like situations in evolution.

5.3. The 'fundamental theorem of cultural selection'

5.3.1 Background

Before describing the 'fundamental theorem of cultural selection', I will give some background on the theory of cultural evolution. The basic principle of this theory is that the 'Darwinian algorithm' (Dennett, 1995) of natural selection is an important

process not only in biological change but also in cultural change. 'Culture', in this usage, means any information that is transferred via social learning from one organism to another. The idea that natural selection acts on cultural traits goes back to Darwin himself (Darwin, 1871), and has been expounded by many scholars since then (James, 1880; Campbell, 1965; Dawkins, 1976; Popper, 1979; Skinner, 1981; Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Hull, 1988; Dennett, 1995). A comprehensive survey of evidence for the existence of natural selection on cultural traits, or 'cultural selection', is given by Mesoudi et al. (2004), and recent work in the field is summarised in Richerson & Christiansen (2013).

In order to derive the Fundamental Theorem of Natural Selection, Fisher had to adapt his Theorem to the complexities of genetic inheritance. However, cultural traits do not reproduce by copying a set of particles in a way analogous to organisms reproducing by copying a set of genes. Therefore, the mathematics of cultural selection can be described by a simple theorem, in which genes do not figure, known as the 'growth-rate theorem', given by Li (1955) and Edwards (1994). The theorem I present here as the 'fundamental theorem of cultural selection' is mathematically almost identical to the growth-rate theorem; what is new is the interpretation of the mathematics to represent cultural selection – the differential reproduction and survival of cultural traits caused by their own characteristics.

Before presenting the theorem I will briefly discuss three previous authors who have combined Fisher's Theorem with cultural evolution in some way. Firstly, Bonner (1980), in the course of a monograph on the evolution of social learning in animals, briefly refers to an equivalent of Fisher's Theorem for cultural evolution created by

his colleague Henry Horn (ibid, p.17). However, this was never independently published or described by Horn. Secondly, Findlay (1990) derived a 'Fundamental Theorem of Natural Selection in Biocultural Populations'; however, Findlay interpreted Fisher's Theorem in the incorrect way that Price (1972) had shown was not Fisher's intention, and thus his theorem has a different meaning to the theorem I present below (though I should make clear that Findlay's Theorem is, to my knowledge, entirely mathematically valid). Finally, Okasha (2007) has investigated a modification of Fisher's Theorem created by considering cultural inheritance in addition to genetic inheritance. Okasha's result is thus concerned with the effect of cultural inheritance on biological evolution, rather than cultural evolution *per se* (and again I emphasise that Okasha's result is, to my knowledge, entirely mathematically valid).

5.3.2 *The theorem*

I will now present the theorem. Imagine a human population. Each individual in the population knows a number of cultural traits, which all together make up a 'population of traits'. Each trait falls into one of a set number of trait-types. There are k trait-types, each of which have absolute fitness f_i (with $1 \leq i \leq k$). Absolute fitnesses have the following meaning: if there are n_i traits of a trait-type i present in the population before selection, there will be $n_i \times f_i$ traits of that type present in the population after selection. From these absolute fitnesses, a relative fitness $w_i = f_i/\bar{f}$ can be calculated for each trait type. Finally, let \mathbf{w} denote the list (i.e. the vector) of all these relative fitnesses, \bar{w} denote the mean fitness of the population of traits, Δ denote the change during one time interval (which may be taken to represent any arbitrary length of time), and $\text{Var}()$ denote the variance of a vector. Then the theorem is

$$\Delta \bar{w} = \text{Var}(\mathbf{w});$$

or in words, ‘the change in the mean relative fitness of the population of traits due to cultural selection is equal to the variance in relative fitness in that population before selection’. An extended proof is given in Appendix G.

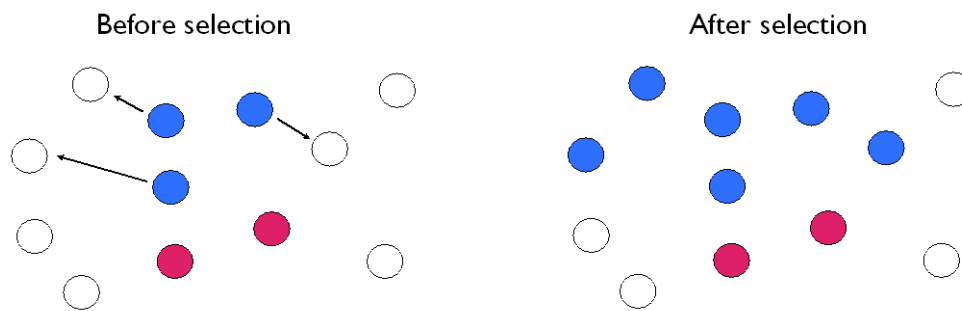


Figure 5.1. An example of cultural selection illustrating the theorem. Circles represent human individuals. Blue and red circles represent people who know one of two different traits, while empty circles represent people who do not know either of these traits.

Figure 5.1 illustrates the meaning of the theorem. The panels depict a human population where each individual (a circle) knows either a trait of the 'blue' trait-type, the 'red' trait-type, or no trait. The absolute fitness of blue traits is 2, and that of the red is 1. The fitness of a trait includes the property of being remembered or retained by an individual through the given time interval, and so the blue traits spread to an additional individual in the time interval while the red traits are simply remembered by their current individuals. In the left panel we see the population before selection, and in the right panel after selection. Before selection, the mean absolute fitness, \bar{f} , was $\frac{3 \times 2 + 2 \times 1}{5} = \frac{8}{5}$, and thus the relative fitness of the blue traits, w_{blue} , was $\frac{2}{8/5} = \frac{10}{8}$ and the relative fitness of red traits, w_{red} , was $\frac{1}{8/5} = \frac{5}{8}$, while the mean relative fitness,

\bar{w} , was by definition 1 (this can be checked arithmetically: $\frac{3 \times \frac{10}{8} + 2 \times \frac{5}{8}}{5} = 1$). After selection, we calculate the mean fitness of the population using the same fitnesses as before selection. Thus, the mean relative fitness after selection, \bar{w}' becomes

$\frac{6 \times \frac{10}{8} + 2 \times \frac{5}{8}}{8} = 1 \frac{3}{32}$. The theorem claims that the increase in relative fitness, $\Delta \bar{w} = \bar{w}' -$

$\bar{w} = 1 \frac{3}{32} - 1 = \frac{3}{32}$, is equal to the variance in relative fitnesses before selection, and

indeed, $\text{Var}(\mathbf{w}) = \frac{3 \times \left(\frac{10}{8} - 1\right)^2 + 2 \times \left(\frac{5}{8} - 1\right)^2}{5} = \frac{3}{32}$.

The intuition behind the theorem can be understood from thinking about Figure 5.1. If there had been more blue traits to start with, then the initial variance in fitness would have been greater, and there also would have been more blue traits after selection, increasing the mean fitness of the population of traits after selection. In general, the more variation is present in the fitnesses of the traits in the population, the more scope there is for the traits with higher fitness to outcompete those with lower fitness, thereby increasing the mean fitness of the population after selection.

Though the above example is simplified, for expository purposes, the theorem also applies in more complicated cases in which people know more than one cultural trait, and/or cultural traits have multiple other cultural traits as ‘parents’ i.e. ‘blending transmission’. In order to incorporate such multi-‘parental’ transmission, fitness must be calculated as follows: if there are x traits of one trait-type, all of which contribute to the reproduction of n traits of their type in other individuals, then their absolute fitness is $\frac{n}{x}$.

5.3.3 Interpretation

In order to interpret the theorem as describing cultural selection, two important definitions must be made. Firstly, fitness must be understood to measure the number of copies of a trait present after reproduction whose reproduction was *causally influenced by some characteristic of that trait*. This causal link is what distinguishes cultural selection from cultural drift. Secondly, cultural traits must be understood to be *ideational*; that is, residing in the mind of an individual, and expressed and transmitted through physical means such as movement, speech, writing, and artifacts. This follows the consensus in the field of cultural evolution (Mesoudi et al., 2004) in viewing the information stored within the individual as the true locus of a cultural trait and the influence of that trait on the individual's behavior and environment as the expression of the trait.

Because of these definitions, the theorem encompasses a number of different cultural evolutionary processes which are not always considered together, and shows that these processes all fall under the umbrella of 'cultural selection'. These processes include:

- the retentiveness of cultural traits, meaning their propensity to be remembered or retained by the individuals who have them;
- content bias (Richerson & Boyd, 2005), where a learner's psychological preferences for and judgements of the distinctive characteristics of a particular trait cause that learner to adopt that trait;
- frequency-dependent bias (Richerson & Boyd, 2005), where a learner uses information about the frequency of different traits within a human population to decide which trait to adopt;

- some forms of model bias (Richerson & Boyd, 2005), where a learner decides to adopt a trait because of a preference for learning from people who have some specified characteristic (e.g. prestige or success in a given domain): namely, only those forms in which the trait that is learnt from the model was causally influential on the model's relevant characteristic (e.g. if having the trait contributed to their success in the relevant domain);
- the natural selection of cultural traits through the differential survival or fertility of the individuals that carry them due to them carrying them (e.g. the growth of pro-natalist religious movements like the Old Order Amish); and,
- cultural group selection, in which the differential survival of human groups with different cultural traits causes the spread of that trait (possible examples include the spread of monogamous marriage, co-operative practices, and military innovations: see Boyd & Richerson, 2010 and Henrich et al., 2012).

Each of these processes are a kind of cultural selection because they are processes in which the characteristics of the cultural traits involved, which may include their memorability, appeal or 'catchiness', popularity, and usefulness – whether through achieving a particular goal in life, increasing survival or fertility, or leading to an increased probability of survival for the cultural group – causally influence their own reproduction and/or survival. This can be reflected formally in recursive models of cultural evolution by the effect of the selective process multiplying the variance amongst the cultural traits.

Classing frequency-dependent bias as cultural selection deserves additional comment. Intuitively speaking, frequency-dependent bias appears not to be like the other processes, since in this process the 'content' of the cultural trait is by definition

irrelevant to that trait's fitness, and its fitness is entirely determined by the frequencies of the various trait-types in the human population. However, from an individual trait's 'point of view', being an instance of, say, the most frequent trait-type in a population of conformers is a characteristic that causes it to reproduce in that population. Since this reproduction is causally influenced by a characteristic of the trait – its being an instance of a particular trait-type, the most frequent one – this is an example of cultural selection.

The theorem, analogously to Fisher's Theorem, quantifies the extent to which these processes of cultural selection adapt the population of cultural traits to the social and cultural environment that they were in prior to selection. The above discussion should make clear that while the theorem shows that the action of cultural selection is always to increase the fitness of a population of cultural traits, it is neutral with regard to the effect of the traits on the biological fitness of the human population. Whether traits tend to work to the benefit or detriment of their carriers' biological fitness is a separate question not addressed by the theorem.

In addition, also like Fisher's Theorem, the theorem is not concerned with a large number of other factors that interact to determine the mean fitness of the population of traits. In the cultural case, these factors include innovation (which includes guided variation [Boyd & Richerson, 1985] and mutation [Cavalli-Sforza & Feldman, 1981]), 'diffusion' (as used by Cavalli-Sforza & Feldman (1981), the cultural equivalent of migration, in which a trait is transmitted into the population from an individual outside the population), change in the social or cultural environments, drift (Neiman, 1995), and the transmission of traits from non-ideational sources (see below).

These factors must be understood with some care. The category of innovation includes processes of blending or continuous inheritance, in which multiple traits from multiple-trait types interact to produce a new trait of a new trait-type. From the point of view of the parent traits, this new trait is a mutation, or innovation, and thus does not count towards their fitness. The trait's 'point of view' also illuminates the meaning of the environment in cultural selection: the 'social environment' of a trait consists of the (mind of the) individual that has the trait and the set of other individuals in the population with which that individual is in contact, while the 'cultural environment' consists of the other cultural traits that the individual and its contacts have. Since the reproduction of a trait must by definition be causally influenced by its own characteristics in order to count as cultural selection, the category of cultural drift includes some forms of model bias (e.g. some forms of prestige or success bias) in which a trait is copied because of some characteristic of a model individual that was not causally influenced by that trait. Lastly, because of the definition of traits as being ideational, the transmission of traits from non-ideational sources – i.e. not from individuals, whether directly or indirectly – is not encompassed by the theorem. For example, a letter from one individual to another in the population may allow a trait from the writer to be transmitted to the reader, and this reproduction may therefore count towards that trait's fitness value. However, if an individual reads a book by a long-dead author and thereby learns a novel trait, this cannot count as an example of the reproduction of a trait, since there was no trait in the population to which this reproduction could rightly be ascribed. However, this latter event is an example of cultural niche construction, an important separate process in its own right (Kendal, 2011), and indeed, the modelling framework of cultural niche construction is

better suited to modelling the transmission of traits from ideational sources such as books, as in this framework there is a clear distinction between the living population of individuals who carry cultural traits and the non-living, niche constructed ecological environment which can separately influence cultural evolution and allow traits to be ‘reborn’ after the death of all their living carriers.

What, then, is the use of the theorem? I suggest that, like Fisher's Theorem, it has conceptual rather than practical value. It mathematicizes the notion of cultural selection, or the differential reproduction and survival of cultural traits, upon which the theory of cultural evolution rests. This rigorous statement brings, in my view, conceptual clarity to the topic, and as outlined above, illuminates the relationships and distinctions between a number of different processes in cultural evolutionary theory.

The literature on cultural evolution is currently divided on the use of the term ‘cultural selection’. Some scholars, such as Cavalli-Sforza & Feldman (1981) use the term habitually, but distinguish it from the differential survival or reproduction of cultural traits through their effects on the biological fitness of their carriers. Other scholars, such as Boyd & Richerson (1985), acknowledge the fact that a Darwinian selective process operates on culture but prefer to discuss more specific processes such as content, frequency-dependent, and model biases. Yet other scholars, such as Sperber & Claidière (2008), have questioned the relative importance of cultural selection in cultural evolution. Therefore I propose that the theorem given above may be used as an objective criterion for the community of researchers in cultural evolution to build a taxonomy or classification of processes in cultural evolution, of which my discussion above provides a ‘first draft’.

5.4. Discussion

In this chapter I have described a new interpretation of the growth-rate theorem (Edwards, 1994) which may bear the title of the 'fundamental theorem of cultural selection'. I have suggested that this theorem can play a similar role in the theory of cultural evolution that Fisher's Fundamental Theorem of Natural Selection plays in the theory of biological evolution. Moreover, I have discussed some ways in which the theorem gives precision to discussions on the processes that make up the theory of cultural evolution.

Lastly, I will deal with the connection between Fisher's Theorem, the 'fundamental theorem of cultural selection', and the Price equation. The Price equation (Price, 1970) is a well-known mathematical equation which can famously be applied to any sort of selection, whether evolutionary or not (Price, 1995). Previous authors (e.g. Rice, 2004; Frank, 2012) have noted that Fisher's Fundamental Theorem can be derived from Price's equation in a very simple way (essentially, by letting the abstract 'trait' in the Price equation be fitness itself, and ignoring the term representing changes in the trait due to transmission). However, this derivation does not make the specific causal links between genes and their average effect that Fisher's (1930) derivation does, and thus also does not invite the idea of viewing natural selection from the 'gene's point of view'. Similarly, while it is possible to derive the 'fundamental theorem of cultural selection' using the Price equation and produce a mathematically identical result, I feel that the concrete interpretation I have given in this chapter is more illuminating with regard to cultural selection.

General conclusions and future directions

This thesis has presented four novel experimental and theoretical models of cultural evolution, divided equally between experimental and theoretical work. In my first experimental chapter, I showed with a novel task that group size can increase the rate of cultural accumulation. This lends support to the models of cumulative culture surveyed in Chapter 1, which have attempted to explain puzzling phenomena such as the loss of technology in Tasmania and the rise of technology in the Paleolithic. In my second experimental chapter, I showed that Acheulean handaxe evolution cannot be fully explained by cultural mutation due to perceptual error. This provides a first example of a transmission chain experiment examining the effects of perception, rather than memory or other cognitive processes, on cultural transmission.

In my first theoretical chapter, I constructed two realistic models of cultural evolution and combined them to produce a model which qualitatively represented the difference between human and nonhuman culture. This extends previously analysed models to encompass the interesting phenomenon of cultural differences, as well as providing a detailed model for the cumulative gap between human and non-human cultures.

Finally in the second theoretical chapter, I offered a mathematical formalisation of the process of cultural selection and argued that this representation can bring theoretical unity to the field of cultural evolution. I believe this theorem will prove useful to discussions amongst both theoreticians and philosophers interested in cultural evolution.

There are many future directions in cultural evolution highlighted by the findings reported here. The experimental examination of cumulative culture in Chapter 2 can

be conducted with tasks in different domains, and greater effort devoted to linking experimental ('toy') tasks to real-life examples of cumulative technological trait-complexes. For example, is cultural accumulation more likely to occur, or faster, with real-life technologies that can be combined easily and additively, as can jigsaw puzzle solutions, compared to real-life technologies that cannot, as represented by paper aeroplane designs? Such work will require detailed historical and/or ethnographic study of the process of invention and innovation. One specific potential type of cumulative culture which may be fruitfully investigated is academic research itself; references to earlier works in papers and books, for example, could allow a clear picture of the 'tree' of cultural traits which make up academic thought, including novel concepts, definitions and terminology, empirical observations, etc.

Experimental tasks of cumulative cultural evolution should also be conducted with different groups of participants, with different designs, and with different incentive structures. One important question to understand is, to what extent does collaboration, or 'skill-pooling', aid the development of cumulative culture? It may prove interesting to link this literature with the literature on cooperation: cumulative cultural evolution can only proceed if traits can be freely copied from previous individuals and built upon, yet in an individually-competitive situation those individuals would have no incentive to share their knowledge. Cultural group selection (see Chapter 1) may provide a solution to this dilemma. Indeed, this might have contemporary implications for the patent system and recent phenomena such as patent trolling, in which companies buy patent rights solely in order to sue inventors who reinvent a technology independently. In addition, the hypothesis that population size affects cultural accumulation suggests looking for phenomena such as technological loss in

the historical record during times of population decrease e.g. due to famine or plague, and technological gain during times of population increase e.g. due to medicinal advances and political changes.

The perceptual experiments of Chapter 3 can easily be applied to other technologies, such as hunting spears, as well as artistic, non-functional objects such as beads (for example, red ochre beads), and the model analyzed therein provides quantitative predictions of the divergence caused by perceptual errors. This model provides a simple baseline against which to detect the signatures of non-random cultural evolutionary processes operating on past material culture, which can be tested in the empirical record. Since there are significant numbers of such artifacts, data on their metric measurements will provide valuable testing grounds for general cultural evolutionary theories of technological change such as this model. The additional advantage of such models is that they are based on well-established psychophysical principles, and these principles could be used to construct other models e.g. models dealing with other sensory domains.

The models of Chapter 4 represent a first step towards combining individual-level models of cultural differences and cumulative culture with quantitative empirical data, which offers much promise for the future. An obvious extension is consider more complicated but realistic models, including models which explicitly track individuals' ages, environmental variables, and spatial location. Additionally, in future models the functional value of traits may be directly modelled, individual heterogeneity may be taken into account, and the multi-level social structure of human communities (i.e. family groups within bands within tribes). Such more complicated models will present

analytical challenges which will have to be faced by more sophisticated computational and/or mathematical techniques. As noted in Chapter 1, one cultural evolutionary model, Bentley's model of random copying, has been rephrased in pure mathematics by Eriksson et al. (2010) as a random walk on the integer partitions of a given number (the population size). Investigating mathematical models of cultural evolution in such ways may unearth deeper insights into cultural evolutionary processes.

Finally, the model of Chapter 5 offers a unifying conception of cultural selection that may focus the debate between researchers in support of, and researchers opposed to the theory of cultural evolution as a whole, as well as clear up conceptual disagreement within the field of cultural evolution over the use of terms such as 'content bias' or 'cultural mutation'. In particular, the term 'cultural selection' has not yet come to be used in a consistent way by different researchers in the field; Cavalli-Sforza & Feldman (1981), for example, use it regularly, while Boyd & Richerson (1985) often use terms referring to more specific processes, such as content, model, and frequency-dependent biases. Since the field of cultural evolution is founded on the borrowing of Darwin's concept of 'natural selection' from evolutionary biology, a coherent, precise, and widely-accepted definition of the term 'cultural selection' will be essential to the growth and wider acceptance of the field.

As noted in the Introduction, cumulative cultural evolution has played a major role in allowing our species to more rapidly adapt to diverse environments and spread across the planet in an evolutionarily short time period. While the biological sciences have been successful in explaining the diversity and complexity of life on the planet, the

social sciences have been less successful in explaining the similar diversity and complexity of human culture. The field of cultural evolution offers a theoretically grounded path to understanding these complex phenomena (Mesoudi, 2011a). As in any science, a combination of empirical and theoretical work is essential, and more specifically, modelling is an essential tool to understand the complicated real world: for especially in social science, we will never be able to isolate every possible contributing factor in the ‘natural laboratory’ of the real world. In this thesis I have presented three modelling studies in which empirical and theoretical considerations are intertwined: in Chapter 2, by testing the empirical predictions of a theoretical model; in Chapter 3, by analysing a previously described theoretical model, deriving testable predictions, and then testing them empirically; and in Chapter 4, by introducing two new models, analysing them, and comparing their predictions with empirical evidence. The thesis is bookended by Chapter 1, which provides a review of the modelling literature that has accumulated so far in the years since the first books of Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985), and by Chapter 5, which provides a mathematical and thus precise description of cultural selection which may be used as the foundation of an ‘ontology’ or classification of cultural evolutionary processes. I hope that these theoretical and experimental models will contribute to a more rigorous and productive science of cultural evolution.

Appendix A.

Full data of the experiment presented in Chapter 2.

Condition	Replicate	Place	Value
Individual	1	1	34
Individual	1	2	27
Individual	1	3	33
Individual	1	4	55
Individual	2	1	57
Individual	2	2	18
Individual	2	3	26
Individual	2	4	44
Individual	3	1	32
Individual	3	2	54
Individual	3	3	58
Individual	3	4	7
Individual	4	1	42
Individual	4	2	60
Individual	4	3	36
Individual	4	4	42
Individual	5	1	49
Individual	5	2	25
Individual	5	3	37
Individual	5	4	54
Group	1	1	41
Group	1	1	37
Group	1	1	47
Group	1	2	70
Group	1	2	38
Group	1	2	48
Group	1	3	33
Group	1	3	47
Group	1	3	79
Group	1	4	36
Group	1	4	61
Group	1	4	55
Group	2	1	69
Group	2	1	57
Group	2	1	55
Group	2	2	66
Group	2	2	57
Group	2	2	88
Group	2	3	82
Group	2	3	67
Group	2	3	27
Group	2	4	80
Group	2	4	98
Group	2	4	95
Group	3	1	50
Group	3	1	23
Group	3	1	32
Group	3	2	56
Group	3	2	28
Group	3	2	29
Group	3	3	50
Group	3	3	48
Group	3	3	57
Group	3	4	100

Group	3	4	43
Group	3	4	52
Group	4	1	52
Group	4	1	38
Group	4	1	38
Group	4	2	31
Group	4	2	56
Group	4	2	59
Group	4	3	52
Group	4	3	62
Group	4	3	36
Group	4	4	41
Group	4	4	62
Group	4	4	44
Group	5	1	44
Group	5	1	23
Group	5	1	10
Group	5	2	2
Group	5	2	48
Group	5	2	26
Group	5	3	40
Group	5	3	36
Group	5	3	51
Group	5	4	57
Group	5	4	25
Group	5	4	25

Appendix B.

Data on the number of distinct pieces completed in the experiment of Chapter 2.

1	2	3	4	5
70	85	65	75	58
73	90	73	82	56
83	83	84	83	72
71	100	100	81	67

Appendix C.

Full data from the experiment presented in Chapter 3.

Chain	Place	Scale	Condition
1	1	1.02038709420869	Larger
1	2	1.0326150299997	Larger
1	3	1.04772486646248	Larger
1	4	1.10165309929125	Larger
1	5	1.13836955677379	Larger
1	6	1.16557555412524	Larger
1	7	1.1734441130667	Larger
1	8	1.16424782215465	Larger
1	9	1.1175095427542	Larger
1	10	1.14666033565637	Larger
2	1	0.972554037845496	Larger
2	2	1.0210288215406	Larger
2	3	1.0523103277033	Larger
2	4	1.03128671079693	Larger
2	5	1.02769543364554	Larger
2	6	1.03333861749822	Larger
2	7	1.08660210349343	Larger
2	8	1.12853423979788	Larger
2	9	1.16029492742365	Larger
2	10	1.15654415801077	Larger
3	1	1.01128640469638	Larger
3	2	1.02038216145833	Larger
3	3	1.005907475327	Larger
3	4	1.02419012728604	Larger
3	5	1.03035489076557	Larger
3	6	1.06349181574041	Larger
3	7	1.03353416581587	Larger
3	8	1.03351419992158	Larger
3	9	1.11402349761038	Larger
3	10	1.13261926177054	Larger
4	1	0.999413274591619	Larger
4	2	1.02908705647786	Larger
4	3	1.04626782596473	Larger
4	4	1.08015112304687	Larger
4	5	1.0968727944114	Larger
4	6	1.12883067460494	Larger
4	7	1.14300645955404	Larger
4	8	1.10868508726178	Larger
4	9	1.12277854225852	Larger
4	10	1.12090985199899	Larger
5	1	1.04846994665897	Larger
5	2	1.04755480402166	Larger
5	3	1.06182642526338	Larger
5	4	1.07441997181286	Larger
5	5	1.04841063620827	Larger
5	6	1.0768203420928	Larger
5	7	1.05295275971384	Larger
5	8	1.06249434315075	Larger
5	9	1.06790791921905	Larger
5	10	1.05270107199929	Larger
6	1	1.00206486280037	Larger
6	2	1.01800234430487	Larger
6	3	0.98306032631614	Larger

6	4	1.0275256060976	Larger
6	5	1.02031298550692	Larger
6	6	1.03769494074041	Larger
6	7	1.03478567504883	Larger
6	8	1.03109292417584	Larger
6	9	0.971202053185665	Larger
6	10	0.957236967144591	Larger
7	1	0.990721181233724	Larger
7	2	1.00602680090702	Larger
7	3	0.982293107466264	Larger
7	4	0.99028251879143	Larger
7	5	0.9766861558394	Larger
7	6	0.975408925836737	Larger
7	7	1.01513453720555	Larger
7	8	1.00634555053711	Larger
7	9	1.01141442131274	Larger
7	10	0.981850451845111	Larger
8	1	1.06026333063299	Larger
8	2	1.02405071836529	Larger
8	3	0.975863854610559	Larger
8	4	0.977514623006185	Larger
8	5	0.996105278246331	Larger
8	6	1.00616738429214	Larger
8	7	1.00957333096591	Larger
8	8	1.02966395337654	Larger
8	9	1.01141759236654	Larger
8	10	1.00191629305753	Larger
9	1	1.06414740175189	Larger
9	2	1.07585387536251	Larger
9	3	1.01507757568359	Larger
9	4	0.97480366562352	Larger
9	5	0.970190134684245	Larger
9	6	1.00631971232096	Larger
9	7	0.96892993441495	Larger
9	8	0.970977143258759	Larger
9	9	0.98800981278853	Larger
9	10	0.979791498357599	Larger
10	1	1.00103380052971	Larger
10	2	0.955388242779356	Larger
10	3	0.95582807968602	Larger
10	4	0.973411103219697	Larger
10	5	0.989152801513672	Larger
10	6	1.00120304084547	Larger
10	7	1.00986964832653	Larger
10	8	1.02838155573065	Larger
10	9	1.04031599287553	Larger
10	10	1.11623513146603	Larger
1	1	0.97385258437648	Smaller
1	2	0.997147732821378	Smaller
1	3	0.964152213356712	Smaller
1	4	0.875708351828835	Smaller
1	5	0.875285896994851	Smaller
1	6	0.862015095566258	Smaller
1	7	0.877776055075906	Smaller
1	8	0.936521236072887	Smaller
1	9	0.943303356748639	Smaller
1	10	0.972686693596117	Smaller
2	1	1.03762623457475	Smaller
2	2	1.03166665002072	Smaller

2	3	1.0191037569913	Smaller
2	4	1.00111894919656	Smaller
2	5	1.0255529757413	Smaller
2	6	0.958790372443922	Smaller
2	7	0.967180217396129	Smaller
2	8	0.890521988377427	Smaller
2	9	0.847049248435281	Smaller
2	10	0.850743995897698	Smaller
3	1	0.964989958792022	Smaller
3	2	0.996467952843868	Smaller
3	3	1.06643361409505	Smaller
3	4	0.998179382324219	Smaller
3	5	1.05207120675752	Smaller
3	6	1.06384803078391	Smaller
3	7	1.05651397057736	Smaller
3	8	1.03382966105143	Smaller
3	9	0.994979789040305	Smaller
3	10	0.95821494362571	Smaller
4	1	1.03432129183683	Smaller
4	2	1.03308939615885	Smaller
4	3	1.03048842736446	Smaller
4	4	1.07907695793383	Smaller
4	5	1.04069898570668	Smaller
4	6	1.03484040508848	Smaller
4	7	1.03225141583067	Smaller
4	8	1.01949097789418	Smaller
4	9	0.99645644309304	Smaller
4	10	0.995590862852154	Smaller
5	1	1.00389597020005	Smaller
5	2	1.03363329060872	Smaller
5	3	0.932629707105232	Smaller
5	4	0.887737568248402	Smaller
5	5	0.915218977494673	Smaller
5	6	0.883711915449663	Smaller
5	7	0.902923979788116	Smaller
5	8	0.919528674501361	Smaller
5	9	0.884367853800456	Smaller
5	10	0.824908128680605	Smaller
6	1	0.991549883293383	Smaller
6	2	1.00257998287317	Smaller
6	3	0.963844738584576	Smaller
6	4	0.954531882083777	Smaller
6	5	0.884840516986269	Smaller
6	6	0.868377697568951	Smaller
6	7	0.8593986825654	Smaller
6	8	0.845253903475675	Smaller
6	9	0.799507870298444	Smaller
6	10	0.862050388220585	Smaller
7	1	1.03932709387577	Smaller
7	2	0.988408308549361	Smaller
7	3	1.00367963386304	Smaller
7	4	0.884898359356505	Smaller
7	5	0.928645747791637	Smaller
7	6	0.928948935768821	Smaller
7	7	0.928821682554303	Smaller
7	8	0.898043316927823	Smaller
7	9	0.91960971254291	Smaller
7	10	0.920930162834399	Smaller
8	1	0.988010400020715	Smaller

8	2	0.996553806189335	Smaller
8	3	1.03400101540305	Smaller
8	4	1.07371928636955	Smaller
8	5	1.06886921830611	Smaller
8	6	1.09395847852302	Smaller
8	7	1.11203606900302	Smaller
8	8	1.10370019068862	Smaller
8	9	1.15381023984967	Smaller
8	10	1.18244004035719	Smaller
9	1	0.959803465409712	Smaller
9	2	0.994103990959399	Smaller
9	3	1.0129216114391	Smaller
9	4	0.985320994059245	Smaller
9	5	0.958314714373964	Smaller
9	6	0.961129788023053	Smaller
9	7	1.01340243715228	Smaller
9	8	1.03424448186701	Smaller
9	9	1.07442032415217	Smaller
9	10	1.12353842070608	Smaller
10	1	1.0063673955744	Smaller
10	2	0.903933725530451	Smaller
10	3	0.89808254403779	Smaller
10	4	0.893241754242868	Smaller
10	5	0.888963239265211	Smaller
10	6	0.977966498172644	Smaller
10	7	0.963611724853516	Smaller
10	8	1.00986025261156	Smaller
10	9	1.03085955810547	Smaller
10	10	1.00977909712358	Smaller

Appendix D.

R source code for the simulation presented in Chapter 3.

```
conditions <- list (  
  "larger" = list ("sd" = 0.0269, "final.mean" = 10.64647, "comparison" = `>=`,  
"final.variance" = 0.6143204),  
  "smaller" = list ("sd" = 0.0399, "final.mean" = 9.700883, "comparison" = `<<=`,  
"final.variance" = 1.33803))  
simulation <- function (condition) {  
  values <- replicate (10000, replicate (10, prod (rnorm (10, 1, condition$sd)) *  
10))  
  mean.p.value <- length (which (condition$comparison (colMeans (values),  
condition$final.mean))) / 10000  
  variance.p.value <- length (which (apply (values, 2, var) <=  
condition$final.variance)) / 10000  
  return (c ("mean p-value" = mean.p.value, "variance p-value" =  
variance.p.value))}  
print (sapply (conditions, simulation))
```

Appendix E.

Supplementary figures for Chapter 4.

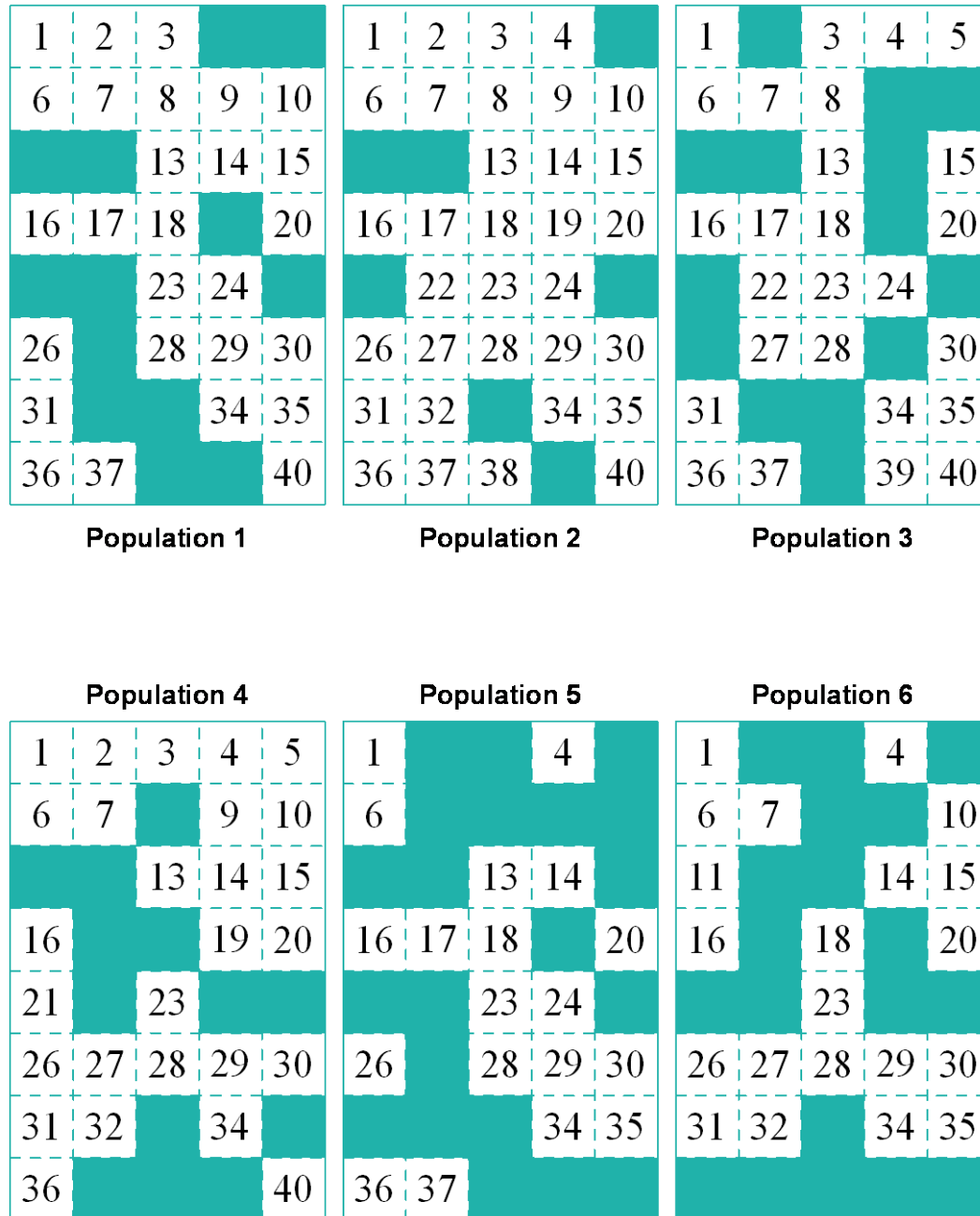


Figure E1. The end result of one simulation of the cultural differences model. Each rectangle represents one population, with numbered cells representing traits present in that population and coloured cells representing traits absent from that population. Parameter values: $N = 100$, $a = 0.9$, $\mu = 0.1$, $m = 0$, $p = 6$.

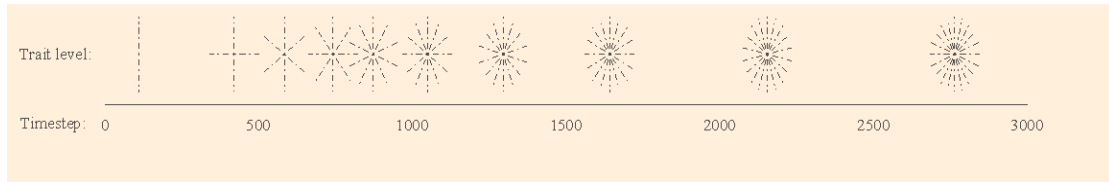


Figure E2. The time course of one simulation of the cumulative culture model. The trait level corresponds to the number of dashed lines making up the star. The mean trait level at any timestep is equal to the trait level depicted by the closest star to the left of that timestep.

Parameter values: $N = 100$, $n = 3$, $a = 0.85$, $\mu = 0.1$.

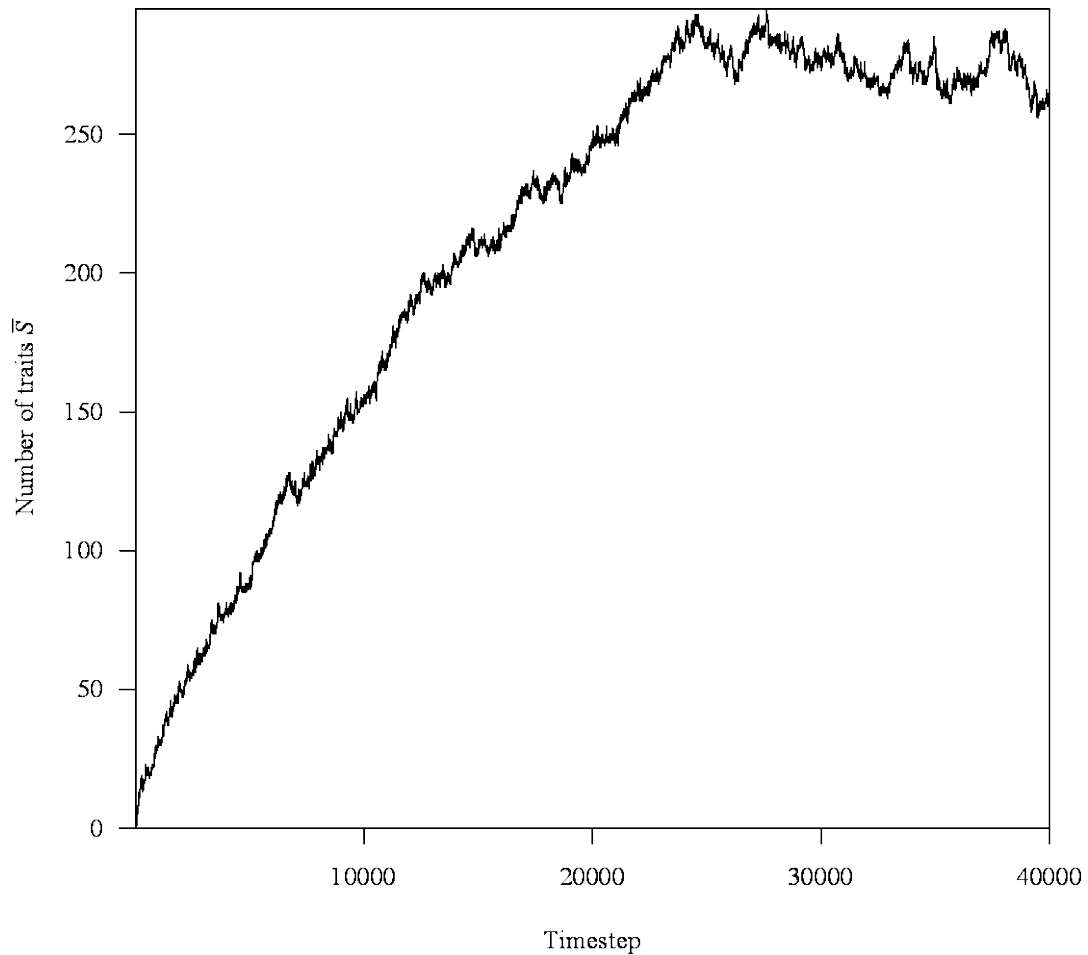


Figure E3. The number of traits known in the population in one simulation of the combined model. Parameter values: $N = 30$, $n = 2$, $a = 0.7$, $\mu = 0.1$, $m = 0$, $p = 1$.

Appendix F.

Proof of result in Chapter 4.

Imagine, in Strimling et al's model (i.e. with $m = 0$), that a focal individual has just invented a new trait. In the next timestep, one of three things can happen: the trait can be lost because the individual dies, the trait can continue to be known only by the inventor, or another individual can learn the trait. Let us denote the probabilities of these three events by p_{lost} , p_{kept} , and p_{copied} . The trait will be lost if the inventor is randomly picked to die; thus,

$$p_{\text{lost}} = \frac{1}{N}.$$

The trait will be learnt by another individual if the inventor does not die, and the individual randomly picks the inventor to learn from, and is successful at learning; thus,

$$p_{\text{copied}} = \left(1 - \frac{1}{N}\right) \left(\frac{1}{N-1}\right) a = \frac{a}{N}.$$

Finally,

$$p_{\text{kept}} = 1 - p_{\text{lost}} - p_{\text{copied}} = 1 - \frac{1}{N} - \frac{a}{N} = \frac{N-a-1}{N}.$$

What is the probability $P(t)$ that the trait is learnt by another individual for the first time exactly t timesteps after it was invented? For this to happen, the trait must continue to be known only by the inventor for $t - 1$ timesteps, and must then be learnt by another individual on the t th. Thus,

$$P(t) = p_{\text{kept}}^{t-1} p_{\text{copied}} = \left(\frac{N-a-1}{N}\right)^{t-1} \frac{a}{N}.$$

Finally, what is the probability that the trait will ever spread beyond its inventor? This happens if $P(t)$ ever happens, i.e. with probability

$$\sum_{t=1}^{\infty} P(t) = \sum_{t=1}^{\infty} \left(\frac{N-a-1}{N} \right)^{t-1} \frac{a}{N}.$$

Using the standard identity for infinite geometric series, this can be shown to be equal

to

$$\frac{a}{a+1}.$$

Appendix G.

Proof of the theorem.

Edwards (1994) gives a concise proof of the general growth-rate theorem. Here I give a more extended proof specific to cultural selection.

Imagine a population of N traits, where each trait falls into one of k trait-types. There are n_i traits of each trait-type, with $1 \leq i \leq k$, and each trait-type makes up a proportion $p_i = n_i/N$ of the population. Each trait of trait-type i has absolute fitness f_i and relative fitness $w_i = f_i/\bar{f}$, where \bar{f} is the mean absolute fitness of the population. The mean relative fitness \bar{w} is thus $\frac{1}{N} \sum n_i w_i = \frac{1}{N} \sum n_i f_i / \bar{f} =$

$$\frac{1}{N} \sum n_i f_i / \frac{\sum n_i f_i}{N} = 1 \text{ (where the summations, like all others here, are from 1 to } k\text{).}$$

Finally, let \mathbf{w} represent the vector of the relative fitnesses of each trait.

The theorem to be proved is that $\Delta \bar{w} = \text{Var}(\mathbf{w})$. Let a variable with an apostrophe denote the value of that variable after reproduction; then $\Delta \bar{w} = \bar{w}' - \bar{w} = \sum w_i' p_i' - 1$.

The point of the theorem, as discussed in the text, is that the mean fitness of the population after reproduction is calculated using the fitnesses of the traits before reproduction, thereby ignoring possible changes in fitness due to environmental change; thus, $w_i' = w_i$. Also, note that p_i' is equal to $p_i w_i$ (to wit, $p_i w_i = \frac{n_i f_i}{N \bar{f}} =$

$$\frac{n_i}{N} \frac{f_i}{\sum n_i f_i / N} = \frac{n_i f_i}{\sum n_i f_i} = \frac{n_i'}{\sum n_i'} = \frac{n_i'}{N'} = p_i'). \text{ Thus, } \Delta \bar{w} = \sum w_i^2 p_i - 1. \text{ But this is exactly}$$

equal to $\text{Var}(\mathbf{w})$, because by definition $\text{Var}(\mathbf{w}) = \mathbb{E}(\mathbf{w}^2) - \mathbb{E}(\mathbf{w})^2 = \sum w_i^2 p_i - 1$.

Therefore, the theorem is proved.

Fisher (1930) defined fitness in a different way, using organismal life and birth tables to define a 'malthusian parameter' m . The theorem could also be derived this way; however, as it is probably impossible to construct accurate survival and reproduction tables for cultural traits, I doubt this would be illuminating.

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