FROM SOCIAL LEARNING TO CULTURE: MATHEMATICAL AND COMPUTATIONAL MODELS OF CULTURAL EVOLUTION

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FROM SOCIAL LEARNING TO CULTURE:

MATHEMATICAL AND COMPUTATIONAL MODELS OF CULTURAL EVOLUTION

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THIS THESIS IS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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CONTENTS

PREFACE

To a great extent the work that constitutes this thesis has been published or is in the process of being published. Therefore the work is presented as a series of individual and relatively independent chapters formed largely from published papers drawn together with a general discussion in Chapter 10. The sections of this thesis are organised to reflect both the progress over time of my work as a graduate student and to reflect the increasing layers of complexity that the modelling techniques I used are capable of considering. Section 1 contains models of the evolution of social learning and social learning mechanisms, Section 2 considers the evolution of social learning strategies and the implications of these strategies for cultural evolution and Section 3 contains three models of human cultural evolution.

ABSTRACT

Humans are unique in the extent and complexity of their cultures. As a species, we generate extensive knowledge and innumerable norms, attitudes, traditions, skills, beliefs and technologies that we share with those around us through teaching, imitation and language. These cultural practices have their roots in our uniquely potent ability for social learning. This thesis sets out to elucidate the process of cultural evolution using a series of mathematical and computational models. These models first investigate the evolution of the capacity for social learning, the rare ability to teach, and the evolution of the smart and strategic use of social learning, in the animal lineage. They go on to investigate the implications of these strategies and mechanisms for culture and find that the form human culture takes is dependant on the amount and nature of social learning as well as on the underlying learning strategies deployed. The thesis also investigates the effect that culture has had on the human evolutionary niche. Cultural practices fundamentally change the selection pressures to which humans are subject and these in turn change both our cultures and our genes through gene-culture coevolution. Finally, a demographic cultural niche construction model is presented, which investigates the application of cultural evolution modelling, cultural niche construction theory and demographic models to the growing problem of sex-ratio imbalance in modern China and considers the implications for policy-making. The analyses presented in this thesis support the argument that the uniquely potent human ability to transmit acquired information through teaching, imitation and other forms of social learning, and through this to shape our cultural and ecological environments, has played and continues to play a central role in human evolution.

INTRODUCTION:

FROM SOCIAL LEARNING TO CULTURE

Material from this chapter has been published as:

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There is a clear conceptual link between the ability to learn strategically and efficiently from other individuals and the human ability to generate vast, complex and diverse cultures (Boyd and Richerson 1985, Rogers 1988, Mesoudi 2011). The ability to acquire cultural norms, beliefs, skills and technology through social learning is a cornerstone of the human species' ecological and demographic success and an undeniable part of what makes us unique as a species. This thesis seeks to understand how humans in particular could have evolved the capacity for extremely efficient social learning and, following from that, how human culture evolved from its simple origins to the vast, varied and pervasive cultural environments we all inhabit now.

Many definitions of the terms 'social learning' and 'culture' exist. Throughout the chapters that form this thesis, I will use a simple definition of social learning, from Hoppitt and Laland (*in press*), adapted from Heyes (1994): 'social learning is learning that is facilitated by observation of, or interaction with, another individual or its products'. Social learning can occur by a number of psychological mechanisms including enhancement effects, imitation and emulation (Whiten and Ham 1992; Heyes 1994; Hoppitt and Laland 2008). Conversely, asocial or individual learning refers to learning that occurs independently of any social influence.

Generating an acceptable definition of culture has long been a bone of contention between researchers investigating the phenomenon from different perspectives (Durham 1991; Brown 2008; Laland and Galef 2009). The definition proposed by Laland and Hoppitt (2003) states that cultures are 'group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information'. This definition is useful here as it allows culture to be viewed on a continuum from social learning and group specific behaviour, such as that seen in Chimpanzee populations (Whiten *et al.* 1999), to more complex human shared beliefs and norms, although these need not be viewed as consanguineous or even, in many cases, as similar at the mechanistic level. In section 3 we consider human culture almost exclusively and move towards a more narrow conception of culture including more human-specific traits like the use of language, cultural norms, institutions and population-specific moral beliefs.

Culture as a phenomenon has had, and continues to have, a profound effect on human evolution (Boyd and Richerson 1985; Richerson and Boyd 2005; Richerson *et al.* 2010; Laland *et al.* 2010). The effect of learning on evolution and evolutionary outcomes has been debated since 1896 when Baldwin proposed that learning might change the speed and outcomes of evolution. Baldwin (1896) suggested that learning 'keeps alive a series of functions' that are not genetic in nature, but that were capable of directly influencing physical heredity. The idea that learned behaviours can influence the outcomes of evolution is now explored in great detail in the cultural evolution, gene-culture coevolution and cultural niche construction literature, each rich in formal theoretical models (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Odling-Smee *et al.* 2003, Richerson and Boyd 2005; Richerson *et al.* 2010).

Modelling Cultural Evolution

Cultural evolution is the application of Darwinian evolutionary principles to patterns of cultural change and diversity, wherein '…individuals characterised by alternative cultural variants differ in their probability of surviving and becoming effective models' (Boyd and Richerson 1985). In 1973 Cavalli-Sforza and Feldman published what was probably the first rigorous mathematical treatment of cultural evolution. They showed that, borrowing from classical genetic models of inheritance, cultural traits could be treated as generally analogous to genes, and could be modelled as evolving through Darwinian processes (with some important modifications accounting for the unique characteristics of cultural transmission such as horizontal and oblique transmission of traits). Cavalli-Sforza and Feldman (1973) suggested that the phenotypes of offspring were in fact interactions between the child's genotype, developmental processes and vertical and horizontal learning. The model they presented formed the basis of an emerging cultural evolution literature and was followed by two influential works: *Cultural Evolution and Transmission* (Cavalli-Sforza and Feldman 1981) and *Culture and the Evolutionary Process* (Boyd and Richerson 1985). These works laid the foundations of cultural evolution and established the field as a mathematically rigorous investigation of cultural patterns and change. The models presented in these books again borrowed their basic structure from traditional genetic models of evolution, extending this structure to include more features of cultural transmission that do not appear in genetic systems (for example transmission biases, one-to-many transmission, guided variation and copy error).

As the field of cultural evolution grew, criticisms of it began to appear (Gould 1991; Pinker 1997; Bloch 2000; Sperber 1996). Some differences between biological and cultural evolution, for example that cultural evolution, unlike biological evolution, allowed for a kind of Lamarkian inheritance (Maynard Smith 1986; Mesoudi 2011) were solved through modifications to genetic models allowing these extra processes to occur (for example through the inclusion of horizontal transfer of traits). However other objections proved more challenging to address. In particular, the use of genetic analogies and methods in modelling cultural change was challenged, as 1) researchers were unable to characterise the exact nature of a *unit* of cultural transmission that could be directly analogous to the gene in genetic evolution and 2) cultural transmission was not considered accurate enough to allow transmission of intact traits (Sperber 1996; Atran 2001).

Parallel to this formal theory, in 1976 Dawkins suggested that cultural traits could be conceptualised as 'memes' that could be retained, inherited and mutated by means that were directly analogous to genetic inheritance. Memes were self-propagating entities selected for features like ‘stickiness’ (propensity to remain in the mind) and ‘catchiness’ (the propensity to be passed from one mind to another) (Dawkins 1976; Blackmore 1999). In this characterisation, the human mind was a meme-machine shaped by the memes to allow their propagation and evolution. The field of memetics relied on rhetorical answers to the problem of particulate cultural evolution and waned quickly (Laland and Brown 2011). Conversely, cultural evolution responded with mathematical investigations. Henrich and Boyd (2002) answered the critics of cultural evolution through a series of models showing that a discrete ‘substrate’ and error-free transmission were not in fact necessary for Darwinian evolution to occur. They showed that features unique to cultural transmission like conformity and prestige bias could compensate for high error rates in transmission and allow the propagation of favourable traits, even in the absence of high-fidelity copying. Deploying another model that assumed continuous rather than discrete mental representations of culture, Henrich and Boyd (2002) showed that a continuous-trait model with strong ‘attractors’ (individual cognitive transformation of cultural traits) and weak selection reduced to a discrete-trait model with weak selection. Henrich and Boyd (2002) succeeded in showing that, at least with respect to the problem of particulate evolution and copy error, the field of cultural evolution was on solid ground in using modified genetic models to reconstruct human cultural lineages, much as geneticists had done for genetic lineages.

To date, social learning and cultural evolution has mainly been modelled using mean-field approaches, for example population genetic models (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981) and non-spatial evolutionary game theory (Maynard Smith 1982). However, recently a number of new and borrowed modelling techniques have been brought to bear on cultural systems. These include reaction-diffusion systems that assume infinite populations (Cavalli-Sforza & Feldman 1981; Kandler & Steele 2009), phylogenetic and cladistics methods (e.g. O'Brien *et al.* 2001; Mace and Holden 2005; Gray and Jordan 200; Gray and Atkinson 2003), interacting particle systems (Hauert 2001; Nowak & May 1992), network-based models (Watts 1999; Franz and Nunn 2009) and cultural demographic models (Powell *et al.* 2009; Li *et al.* 2000). These various methods are useful in different circumstances, depending on the scale and level of detail required in answering specific questions (Levins 1966). They may also give different results when applied to the same problem (Durrett and Levin 1994). Thus, the choice of method goes deeper than pure mathematical or computational convenience.

The choice of model type forms a theme running through a number of chapters in this thesis. In particular, I explore how factors like the inclusion of assortment, spatial structure or population structure in cellular automaton models and population genetic models ultimately influences the outcome of the models and their explanatory power. Of course the technical problems involved in implementing spatial, cellular automata-based simulation models were in the past prohibitive but have been greatly reduced as more powerful computers have become available. The availability of simulation software like NetLogo makes spatially explicit cellular automata models easy to construct and analyse, while more flexible programming environments like Python, Wolfram Mathematica and MATLAB (used throughout this thesis) facilitate the construction of complex and bespoke models.

Partially as a result of these technical limitations, early spatial models were largely analytical. Cavalli-Sforza & Feldman (1981) briefly considered the effects of spatial structure on cultural transmission systems. They examined the spread of information across a spatially stratified population, rather than the effects of space on the evolution of traits. Nonetheless, this analysis gave valid insight into the dynamics of the invasion of social learning and innovation (or defection and cooperation), allowing them to characterise the invasions as waves spreading in fronts, following reaction-diffusion dynamics.

The 'interacting particle' or agent-based approaches used in Chapters 2, 4, 5, 6 and 7 are simulations in which computer agents are free to interact, reproduce, and, in this case, learn under strict conditions in controlled environments. In Chapters 4, 5 and 6 (covering the Social Learning Strategies Tournament), interactions are free and random between any two (or more if the parameters allow learning from many role models) individual members of the population. This type of model is a close parallel to the agent-based modelling framework (but not the strategic game) used by Axlerod (1980), which gave important insights into the population dynamics and evolution of cooperation. In Chapters 2 and 7 (models of the evolution of social learning and cultural niche construction respectively), this agent-based approach is extended to include spatial structure with a cellular automaton grid structure and imposing Moore neighbourhood (closest eight neighbour) interactions. This modelling framework is applied to the evolution of social learning in the first spatially explicit model of Rogers' paradox presented in Chapter 2.

Social Learning Strategies and Rogers' Paradox

A simple model proposed by anthropologist Alan Rogers (1988) is often used as a tool for investigating the evolution of social learning in general and of social learning strategies in particular (Rogers 1988; Boyd and Richerson 1995; Enquist *et al.* 2007). The model assumed that there were two behavioural traits available to learn, matching two possible environmental states. For each of the individuals in his population, choosing the correct behaviour for the current environment yielded a fitness payoff. Rogers' model was a simple thought experiment resting on a series of basic assumptions and lent itself well to spatial extensions (Chapter 2) as well as extensions dealing specifically with different transmission biases and social learning strategies (Boyd and Richerson 1995; Enquist *et al.* 2006).

This model led to one of the most influential ideas in the study of the evolution of social learning to date, known as Rogers' Paradox. Rogers (1988) found that when social learners (who copy the behaviour of a randomly selected member of the population) are in a minority, their fitness is higher than that of the asocial learners who directly sample the environment and who thus have a constant fitness. However, the fitness of social learners is frequency dependent and declines as the proportion of social learners increases (Figure 1.1A). This happens because as asocial learners decline in number there are fewer individuals producing accurate information about the appropriate behaviour to perform in the current environmental state (Figure 1.1B). Eventually, the population evolves to a mixed equilibrium where the fitness of social learners equals the fitness of asocial learners. In other words, contrary to the notion that copying increases absolute fitness, the average fitness in a mixed population at equilibrium is the same as it would be in a population of solely asocial learners. (Giraldeau *et al.* 2003; Henrich & McElreath 2003).

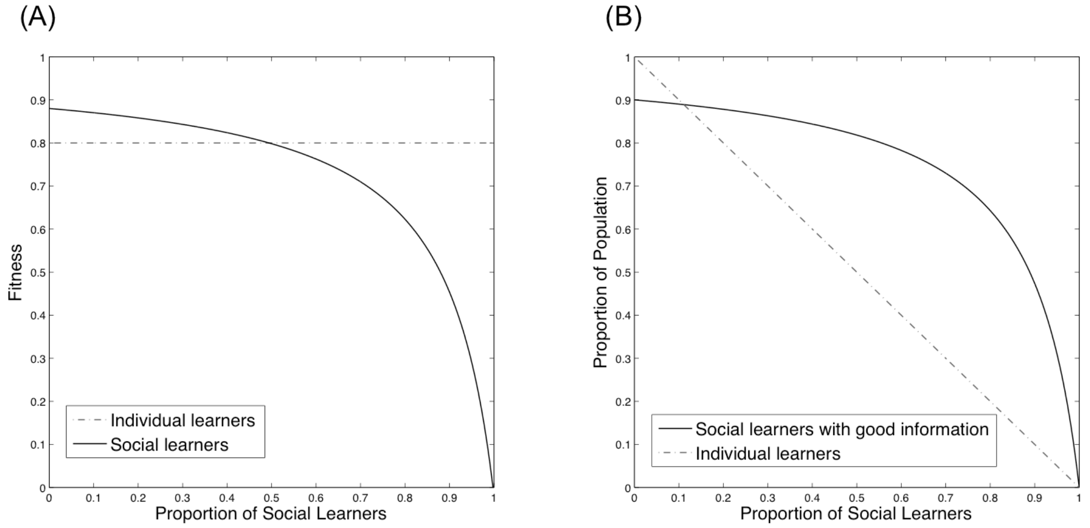

Figure 1.1. Results from Rogers (1988): (A) As the frequency of social learners increases in the population, the fitness of social learners declines while the fitness of asocial learners remains constant and (B) as the frequency of social learners in the population increases and the number of asocial learners decreases, the frequency of social learners with correct information declines.

It is a testament to the surprise with which this result was met, that the effect Rogers detected was called a paradox, when strictly it is a non-paradoxical consequence of the frequency dependence of social learning in a population. While it was widely assumed that, as the basis of culture, social learning must be adaptive, Rogers showed that this need not be the case and that our understanding of the evolution of social learning was incomplete.

In 1995 Boyd and Richerson attempted to recover Rogers' original finding using models with a number of different sets of assumptions to ensure that the paradox was not an artefact of the model's simplicity. Boyd and Richerson introduced spatial variation in the environment, allowed asocial learning errors to occur, allowed strategic choice of high-fitness role models and thus what they termed 'biased transmission', and extended the model to include more than two behavioural traits. Each of these extensions led to the same robust result: social learning did not increase the mean fitness of the population. This finding resembles the producer-scrounger frequency dependence observed in social foraging models with social learners acting as information parasites (Barnard and Sibly 1981; Giraldeau and Caraco 2000; Giraldeau *et al*. 2002). Boyd and Richerson (1995) reasoned that Rogers' result would arise in any evolutionary game where social and asocial learners played against each other and the value of the learned information remained frequency independent. They suggested that cumulative culture or strategic combinations of social and asocial learning would solve the paradox, allowing culture to be fitness enhancing.

There have now been many proposed solutions to Rogers' paradox (discussed at length in Chapters 2, 4 and 10). One of the most important and general of these solutions is the selective use of social and asocial learning embodied in the concept of 'social learning strategies' (Aoki & Nakahashi 2008; Boyd & Richerson 1985; Henrich & McElreath 2003; Laland 2004; Kendal *et al.* 2009). The key idea is that natural selection is expected to fashion evolved psychological rules that specify when an individual should copy others and from whom they should learn.

According to this argument, the blind, random social learning that was assumed in Rogers' original model is replaced by more strategic copying, which combines interaction with, and learning directly from, the environment with the use of social information ('when' strategies or direct biases e.g. Table 1.1A). Directed social learning where individuals learn strategically from carefully chosen role models like those who are older or more successful ('who' strategies/indirect biases e.g. Table 1.1B) or where individuals attend to the frequency of traits within populations (frequency dependent biases Table 1.1C) have also been explored both theoretically and experimentally and many have been shown to confer fitness benefits (Boyd and Richerson 1988; Boyd and Richerson 1995).

Table 1.1 Example social learning strategies/ biases

(A) Direct biases and 'when' strategies	**Theoretical support**	**Empirical evidence**
Copy when dissatisfied	Schlag 1998	Galef *et al.* 2008
Copy when asocial learning is costly	Boyd and Richerson 1985	Templeton and Giraldeau 1996
Copy when uncertain	Boyd and Richerson 1985	Galef *et al.* 2008; McElreath *et al.* 2005
Copy when payoffs drop	Chapters 4, 5 and 6, this thesis	Grüter *et al.* 2010; Seeley and Town 1992; Biesmeijer and Seeley 2005
(B) Indirect bias		
Copy successful individuals	Laland 2004; Henrich and Gil-White 2001	Coolen *et al.* 2003; Hewlett and Cavalli-Sforza 1986; Mesoudi and O'Brien 2008
Copy kin	Boyd and Richerson 1985; Boyd and Richerson 1988	Griffiths 2003; Franks and Richardson 2006; Von Frisch 1967
(C) Frequency-dependent bias		
Copy the majority	Henrich and Boyd 1998	Chou & Richerson 1992; Lefebvre & Giraldeau 1994
Conformity bias	Boyd and Richerson 1985	Morgan *et al.* 2012

Enquist *et al.* (2007) extended the Rogers model to allow a social learning strategy '*critical social learning'* to play the evolutionary game outlined by Rogers with social learners and asocial learners. *Critical social learners* would use social learning first and would use asocial learning only if social learning failed to give the right answer. Enquist *et al.* also adjusted the regime of environmental change ensuring that changes in the environment could not reverse previous changes. Rogers' model assumed that those partaking in individual learning always found the correct solution for the environment at that time. Enquist *et al.* (2007) relaxed this assumption too, by introducing a parameter describing the efficacy of asocial learning, which varied between 0 and 1. This more general model found that the combination of adaptation and inventiveness offered by *critical social learning* led to a solution of Rogers' paradox in which critical social learners always out-competed pure social learners and under most circumstances, asocial learners as well.

Enquist *et al.* claimed that the success of *critical social learning*, was due to the adaptive evaluation and filtering of information. The individuals deploying the *critical social learning* strategy necessarily evaluated the adaptiveness of the solution they had obtained and, using this information, they then decided whether to learn again (this time through asocial learning). Whether or not their results hold when individual learners, for example, were given a similar capacity for evaluation and a second chance to learn individually was not examined even though the importance of the filtering effect itself was repeatedly stressed. The real advantage to conditional strategies like critical social learning and its converse '*conditional social learning'* where individuals first try asocial learning and use social learning only if this fails, is that they do not lead to the fitness depression associated with pure social learning. *Conditional social learning* was also found to be a similar solution to Rogers' paradox (see Chapter 2; Enquist *et al.* 2007). A potentially contentious feature of these two strategies is that they effectively get an extra round of learning for free, relative to pure strategies as well as having a sense of the optimality of their behaviour before deciding to learn again.

Chapters 2, 4, 5 and 6 investigate the circumstances under which one would expect social learning strategies to be favoured by natural selection and what forms these strategies might take.

Chapter 2 is a cellular automaton model of the evolution of social learning strategies that pays particular attention to the effect of space on the results and implications of Rogers' paradox. This model shows that the presence of space, while providing one possible solution to the original paradox, also introduces another counterintuitive finding that the original Rogers model failed to detect: that space can allow social learners to increase in frequency, even as they reduce overall fitness.

Enquist *et al.* (2007) assumed that the fitness functions associated with behavioural traits were discrete, meaning that a solution matching the environment gets the maximum fitness payoff and any other solution gets no fitness payoff at all. The simulation model presented in Chapter 2 replaces this binary fitness payoff with a payoff distribution in which the best solution is rewarded with a maximum payoff while others getting progressively further away from the ideal are rewarded with a lower payoff tending towards zero. In other words, the model assumes that behaviour can be aligned on a continuous distribution that specifies its degree of match to the environmental context. This payoff distribution allows the model to capture the 'harshness' of an environment, with a harsher environment giving a steeper decline in payoffs when moving away from the best solution (Figure 1.2).

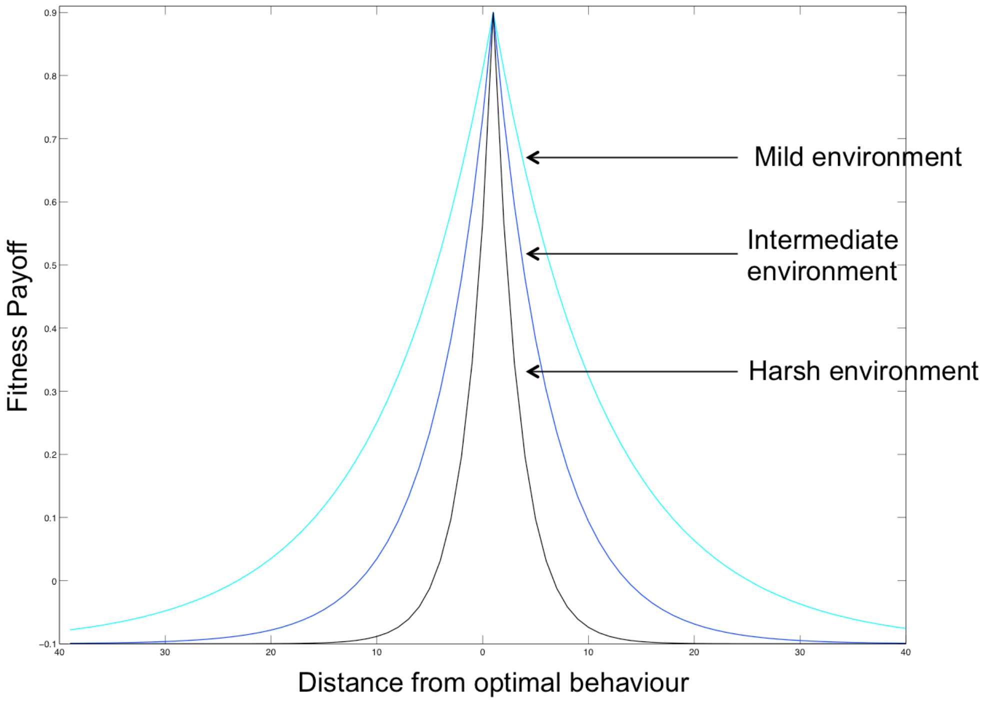

Figure 1.2: The ‘harshness’ of an environment as modelled in Chapter 2. A harsher environment penalises behavioural distance from the optimal behaviour more harshly than a milder environment.

Chapter 2 compares the relative effectiveness of asocial learning, random social learning and the two aforementioned strategic forms of social learning -*conditional social learning* and *critical social learning*. The analysis shows that while social learning strategies provided solutions to Rogers’ paradox there were conditions under which it is reasonable to expect random social learning to be favoured, such as a high cost of asocial learning in a relatively harsh environment with few behavioural traits to choose from. As discussed in Chapter 2, this is similar to the idea of neutral drift in practices like pottery making, where the chances of producing something aesthetically pleasing may be low, but there are a range of examples available to copy, all of which have previously been selected because they are, to some degree, pleasing.

The Social Learning Strategies Tournament

As described above, much recent empirical and theoretical work now supports the idea of selective and strategic use of social learning (Boyd and Richerson 1985; van Bergen *et al.* 2004; Kendel *et al*. 2009). This has led to the question of which strategies are best to use and when is best to use them. This would have been intractable to address as an analytical problem and difficult to address using standard simulation approaches. The Social Learning Strategies Tournament provided a means to compare the effectiveness of a large number of strategies in a standard environment.

The tournament was a large-scale, computer-based, open competition run and analysed between 2008 and 2009. It invited participants to submit learning strategies that they thought would best enable hypothetical agents to survive in a complex and changing simulation environment. Agents using different strategies competed in a virtual environment, first in a round-robin competition and finally in a melee with a series of changing environmental parameters (full details are given in Chapter 4). Chapter 4 presents the original tournament analysis and examines what features of the strategies contributed to their success (such as timing of learning moves, level of environment estimation and amount of social learning), and what mixture of social learning, asocial learning and exploiting those acts to gain fitness benefits was optimal.

Chapter 5 goes on to examine what types of cultures different strategies generate, in terms of how many cultural traits the population could innovate and maintain, how long these cultural traits remained in the population and how evenly spread those traits were among individuals. The analysis showed that strategies relying on social learning to different extents could create cultures with different characteristics and importantly that (as discussed in Chapters 5 and 10) an increased reliance on social learning alone could generate cultures that mimicked some key characteristics of human culture such as large amounts of cultural knowledge persisting for long periods of time, some semblance of conformity and rapid turnover in behaviour.

The effects of the use of memory and future planning in the ultimate success or failure of the strategies in round 1 of the tournament are examined in Chapter 6. Here the analysis focussed on the first (round -robin) round in order to consider the types of memory and future planning used by successful as well as less successful strategies. The top ten strategies from stage 1 made generally made good use of their access to memory where lower ranking strategies did not. Although the tournament did not specifically hard-code the ability to use mental time travel, some strategies engaged in behaviour that was similar to mental time travel as defined in animal research (Clayton *et al.* 2003), with aspects of discounted memory and future planning. The agents used their memories of past returns on behaviour to predict future changes in the environment, relating these predictions to their future moves.

The Evolution of Teaching

Certain high-fidelity forms of social learning (such as teaching and imitation) are thought to contribute to the particular success of human social learning (Boyd and Richerson 1985; Dean *et al.* 2012; Enquist *et al.* 2010) and are useful to investigate in close detail. Chapter 3 presents a mathematical model of the evolution of teaching, a uniquely cooperative form of social learning. Unlike other social learning mechanisms, when teaching, demonstrators pay a cost to impart information to their pupils. This cost raises the interesting question of when it pays to engage in costly information donation and when the costs outweigh the inclusive fitness benefits. Caro and Hauser (1992) proposed a functional definition of ‘teaching’ applicable to animals, in which a tutor is said to teach if it 1) modifies its behaviour in the presence of a pupil, 2) suffers some cost, and 3) promotes the pupil’s learning. Using this definition, researchers have reported putative cases of teaching in species including ants, bees, pied babblers, meerkats, and cats (Franks and Richardson 2006; Leadbeater *et al.* 2006; Thornton and McAuliffe 2006; Raihani and Ridley 2008; Rapaport and Brown 2008).

Perhaps the most compelling example of animal teaching occurs in the meerkats of the Kalahari (*Suricata suricatta*) (Thornton and McAuliffe 2006). Meerkats are obligate cooperative breeders and their groups contain one breeding pair and between 2 and 40 ‘helpers’ who provision young pups with food. Some of the prey items available to the meerkats, for example scorpions, are dangerous and information on how to safely process and eat them must be learned. Meerkat helpers kill these dangerous prey items before presenting them to pups when these pups are very young. As the pups grow, the helpers provide progressively more mobile and dangerous prey items (for example an immobilised scorpion with the sting removed, followed by a mobile scorpion with no sting, followed by a full live scorpion). In this way meerkat pups are shaped to learn how to deal with this prey demonstrably faster than if they were provided with live scorpions from birth (Thornton and McAuliffe 2006). Thornton and McAuliffe showed that meerkat helpers were attentive to the age of the pups being provisioned and showed, through playback experiments, that more intact food items were delivered to older pups and more attenuated food items were brought to younger pups. When the begging calls of young meerkats were played to the helpers they processed the food significantly more than when the begging calls of older pups were played. Overall, the behaviour satisfies the three conditions for teaching specified by Caro and Hauser (1992) since the authors show through a series of experiments that the teachers modify their behaviour in the presence of naïve conspecifics, that providing the pups with processed food and later with mobile prey is considerably more costly to meerkat helpers in terms of time than providing only dead prey and finally, that meerkats taught in this way were significantly more likely to safely process a live scorpion as compared to their untaught companions (Thornton and McAuliffe 2006).

Other cases of animal teaching include the tandem running behaviour of the ant *Temnothorax albipennis* (Franks and Richardson 2006). These social insects use tandem running to guide their conspecifics to new nesting sites when their current site is no longer inhabitable or to new sources of food. Although the guide ants can (and sometimes do) carry their naïve conspecifics to the new location, this inhibits learning as the naïve ants are carried upside down and facing backwards, unable to orientate themselves or attend to landmarks. When tandem running, the naïve ant is in contact with the guide ant's abdomen at all times, when contact is lost the guide ant stops and waits until contact is re-established before continuing on the journey allowing time for the pupil to attend to landmarks and learn the route. This was shown to quadruple the time taken to reach the new location, representing a considerable time cost in comparison to carrying, and satisfying Caro and Hauser's condition that a costly change in behaviour must occur in the presence of a naïve conspecific. Caro and Hauser's final condition for teaching was that the change in behaviour must enhance the pupil's learning. In the case of tandem running ants, ants that were guided to a new location certainly learned the route they should take, although it was not demonstrated experimentally that they could find the location more quickly than naïve individuals. The case of tandem running ants led Franks and Richardson (2006) to propose an addition to the definition of teaching. As well as demanding a costly change in behaviour and enhanced learning, they proposed that feedback between teacher and pupil (such as the abdomen tapping and contact seen between teacher and pupil ants) was also a necessary condition for teaching.

A putative case of animal teaching was also reported in another social insect, the honeybee (*Apis mellifera*). The bees engage in a 'waggle dance', which has been decoded by researchers and contains geographic information on the distance, direction and quality of nearby food sources and nesting sites (vonFrisch 1967; Seeley *et al.* 2000). This dance occurs in view of naïve workers who then gain information about the location of the food source.

More recently, it has been shown that the bees may also engage in a kind of feedback in some circumstances, giving ‘stop signals’ to the dancing bees when a sufficient number of naïve bees have witnessed dances, gained information and moved to a new nesting site (Seeley and Visscher 2004).

While cases of animal teaching remain controversial, and their relationship with human teaching is unclear (Csibra 2007; Leadbeater *et al.* 2006; Premack 2007), these cases of teaching raise a number of questions that Chapter 3 endeavours to answer: ‘What do these species have in common that led to the evolution of teaching?’; ‘Why is teaching not more widespread in animals?’; ‘Why is it that intelligent animals such as chimpanzees seemingly do not teach if ants and bees are capable of doing so?’, and finally ‘How did a very general capability for teaching evolve in the human lineage?’.

The model presented in Chapter 3 is an investigation of the evolution of teaching using analytical population genetic models, which may have implications not only for our understanding of the evolution of social learning but also for the search for the evolutionary roots of human cooperation and cumulative culture. While most teaching meets current definitions of cooperation (West *et al.* 2007), it being favoured in the tutor because it promotes the acquisition of fitness-enhancing information in the pupil, certain unique features specific to teaching render a specialised treatment necessary. These include the fact that taught information can be acquired through means other than teaching (e.g. through trial-and-error learning or inadvertent social learning), and that the dynamics of information transfer differ considerably from the dynamics of the spread and accumulation of physical resources. These differences mean that the evolution of teaching is not explained by contemporary theory of the evolution of cooperation (Sachs *et al.* 2004; Lehmann & Keller 2006; West *et al.* 2007).

While there has been extensive research into topics such as the evolution of social learning (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Feldman and Zhivotovsky 1992), learned communication (Boyd, Gintis and Bowles 2010; Kirby, Cornish and Smith 2008; Kirby, Dowman and Griffiths 2007), and learned cooperation (Boyd and Richerson 1985; Fehr and Fischbacher 2003; Gintis 2003; Boyd *et al.* 2003, Peck and Feldman, 1986), Chapter 3 represents the first step towards a formal theory of the evolution of teaching.

Cultural Niche Construction

Finally, Chapters 7, 8 and 9 make the transition from the evolution of social learning to cultural niche construction. Niche construction is a process by which an organism alters the environment in which it exists and thereby modifies the selection pressures to which it, and other species, are subject (Lewontin 1983; Odling Smee *et al.* 2003; Laland *et al.* 1999). This encompasses both ecosystem engineering in which the organism alters its environment - a beaver building a dam for instance, or a bird building a nest - and the evolutionary feedback from the changed environment to the constructor, its descendants, and other organisms that cohabit its environment. Niche construction theory, unlike more traditional models of evolution, considers both ecological and genetic inheritance.

Humans are particularly potent niche constructors, not least because the transformations that they bring about in environmental states are reliant on cultural knowledge (Odling-Smee *et al.* 2003, Smith 2007, Laland *et al.* 2000, Laland *et al.* 2010, Laland and O'Brien 2010). Even in the absence of culture, analytical genetic models of niche construction (Laland *et al.* 1996; Laland *et al.* 1999; Kylafis and Loreau 2008) were successful in showing that organisms could, through their own actions, alter the course of their evolution. Such models showed that niche construction could allow accumulation of beneficial resources which could favour costly niche constructing traits through inclusive fitness effects (Lehmann 2008), allow organisms to alter their environments rendering harsh environments habitable in the long term through resource creation (Kylafis and Loreau 2008) and alter the ability of species to coexist in one ecological niche either by driving niche constructors to extinction through a 'tragedy of the commons' in resource creation and use, or by promoting polymorphic, specialised niche constructors (Krakauer *et al.* 2009).

Although, generally, niche construction is considered to be ecological in nature, it is also true that much human niche construction is uniquely reliant on cultural traits. Where cultural practices alter the selection pressures on the human genome they may thereby be regarded as cases of niche construction. It is important to understand the impact that these changes have on human evolution and genetic variation. The details of this interaction are also of relevance. For example, if cultural traits are transmitted through vertical transmission will this generate genetic variation that is qualitatively different to that produced by horizontal transmission? What difference if any does the inclusion of realistic assumptions about spatial interactions make?

Early niche construction models adopted a two-locus population genetic approach (Laland *et al.* 1996; Laland *et al.* 1999), with each individual genotype having two loci, a niche-constructing locus, **E**, and a resource-dependent 'recipient' locus, **A**. Each of these, in turn, had two possible alleles: at the **E** locus *E*, a niche constructing allele and *e* a non-niche constructing allele, and at the **A** locus *A*, an allele that increased in fitness with a change in resource frequency (thus affected by local niche constructing activity) or *a*, an allele that decreased in fitness. These models, however, rested on strict assumptions of infinite population size and lack of stochastic processes.

Silver and DiPaolo (2006) developed a spatial version of these models. They assumed finite populations in a simulation framework, allowing a certain amount of stochasticity to affect the population dynamics. They also situated the populations in a spatially stratified, cellular automaton framework. These alterations actually increased the parameter space across which niche construction and recipient alleles could survive and become fixed in a population. Silver and DiPaolo (2006) suggested two reasons why the effects of space made such a profound difference to the outcome of the model in terms of both likelihood of alleles fixing in the population and the range of parameter values over which fixation was possible. Firstly, clustering buffered costly alleles for a time, allowing them to become established in the population and to spread when conditions improved through their own niche construction (Chapters 7 and 10). Secondly, a localized resource distribution allowed strong linkage disequilibrium (a non-random association of independent alleles) to form between niche constructing traits and recipient alleles. In other words, niche-constructing traits can spread by creating conditions that favour their own hitchhiking. The models presented in Chapter 7 extend Silver and DiPaolo's analysis using spatially explicit gene-culture co-evolutionary models to investigate whether, and under what circumstances, cultural niche-constructing practices can run away with genetic variation. The models also ask to what extent this dynamic is affected by cultural transmission biases operating against the niche-constructing trait, a viability cost to the genotype favoured by cultural niche construction, and the cost of cultural niche construction, modelled as a viability deficit to the cultural practice.

Cultural evolution and society

The insights into gene-culture coevolution driven by niche construction are of potential importance to the understanding of recent human evolution. However the processes that underlie cultural change itself are also of interest. Cultural niche construction can drive culture-culture interactions where the frequency of one trait in a population can alter the frequency of another. Chapter 8 is a general model of cultural niche construction capable of considering both the kind of gene-culture process discussed in Chapter 7 and these culture-culture interactions. The model can be used, as described in the discussion of the chapter, to examine the cultural evolution of such diverse systems as religion and fertility, the evolution of large-scale conflict and the evolution of sex ratio bias in Asia and North Africa. Although spatial effects are not explicitly modelled here, it is important to note that the effect of space is to restrict free and random association and interaction between individuals. Here this is achieved through the introduction of assortative mating. This implies a kind of population structure resting on the assumption that similar individuals may be more likely to interact with each other than with less similar individuals (Cavalli-Sforza and Feldman 1981). The effects of positive assortative mating are similar to the effects of local reproduction and dispersal in an agent-based model: individuals are more likely to reproduce with those sharing their traits.

Through the lens of cultural evolution we can examine both human evolution in the recent past and the evolutionary trajectory we find ourselves taking now. It is easy to see every-day examples of how culture has altered the selective pressures to which we, as a species, are subject. For example it is clear from both empirical and theoretical work that genes for lactase persistence coevolved with human dairy farming practices in the recent past (Simoons 1970; Aoki 1986; Feldman and Cavalli-Sforza 1989; Durham 1991). The evolution of cooperation has also been modelled using cultural evolutionary approaches showing that the current high levels of human pro-sociality may be the result of gene-culture co-evolution between genetic predispositions toward cooperation and cultural norms enforcing it (Boyd *et al.* 2003; Fehr and Fischbacher 2003; Gintis 2003). This has led to the emergence of the idea of ‘cultural group selection’ where populations maintain cultural boundaries through transmission of norms and beliefs among its members and through strong reciprocity (a combination of indirect reciprocity and punishment that maintains cooperation), and groups displaying advantageous cultural traits outgrow other groups (Boyd and Richerson 1985). In this way in-group cooperation is fostered along with out-group conflict.

Cultural group selection can potentially favour what Richerson and Boyd (1998) termed 'tribal instincts' such as hostility to out-group members and in-group altruism. This raises the possibility that cultural evolution and gene-culture coevolution may also allow us to examine some of the more harmful aspects of human culture like the human propensity to wage large-scale, highly organised war, which is unequalled in the animal kingdom (Choi and Bowles 2007; Richerson and Boyd 1998; Bowles 2009). The evolution of in-group altruism and parochialism in the human lineage was investigated using an agent-based simulation model by Choi and Bowles (2007), who found that under conditions present in the late Pleistocene, the coevolution of altruism and parochialism was plausible. Bowles (2009) shows with archaeological evidence from early humans that the levels of inter-group conflict seen in hunter-gathers of the Pleistocene was sufficient to allow the evolution of in-group altruism through cultural group selection. This analysis was extended in an analytical framework to include life history features of populations (such as group size, migration rates and division of labour between sexes in society) by Lehmann and Feldman (2008) who showed that the selection pressures on traits such as belligerence and increased fighting ability, which they termed 'bravery', which endowed combatants with a higher probability of success in conflicts, could be substantial. The analysis showed that tribal warfare was a response to a lack of resources for both combatant and non-combatant members of society since the resources gained through warfare benefitted all of society and did not increase conflict within a society.

However as Hinde (1997) points out, the evolutionary forces that supported small-scale conflict in tribal societies are unlikely to be the same in the large-scale industrial conflicts we see today. Rather it is the culturally driven exploitation of genetic predispositions towards self-defense that leads to modern large-scale conflicts. The model in Chapter 8 briefly investigates paramaterisations of a cultural niche construction model designed to reflect modern, as opposed to ancestral, warfare. Under these conditions, the model shows that a predisposition toward warfare alone cannot fix in the population and that for a given set of parameters there is just one polymorphic equilibrium between peaceable and warlike traits.

As discussed in Chapter 10, cultural niche construction modelling has the potential to become a useful tool in guiding cultural policy makers. Chapter 9 again addresses the problem of sex-ratio skew in Asia and North Africa, concentrating especially on the implications of changes in policy governing reproduction in China. The sex-ratio at birth (SRB) is the ratio of live male births to live female births. This has been found to be about 1.05 for most large human populations (Coale 1991). The SRB can be dramatically elevated by practices reflecting a cultural bias toward preferences for male children. These practices include widespread gender-based infanticide of girls or sex-selective abortion of female foetuses. The human cost of these practices is estimated to range from 60 million (Coale 1991) to 107 million (Sen 1990) worldwide and this skew in SRB has been reported in India, Bangladesh, China, Pakistan, Nepal, South Korea, Afghanistan, and across parts of North Africa (Croll 2000; Das Gupta *et al.* 2003; Klasen and Wink 2003). Although the results are similar, the root causes of the skew in SRB in each of these regions are different. While India and China have two of the worst sex ratio problems globally, the societies in which the problems arose are substantially different in terms of governmental structures, enforced restrictions on reproduction and marriage practices, but are somewhat similar in the status of women in society or access to education (Croll 2000). The wide differences between societies sharing similar problems means that models of the skew in sex-ratio need to be specifically targeted to a particular societal structure. Chapter 9 concentrates on the sex-ratio skew in

China, investigating the interaction between marriage practices, patriarchy and government mandated restrictions on reproduction. The model uses cultural niche construction, coupled with traditional two-locus cultural evolution models and demographic Leslie matrix modelling to estimate the possible impact of policy intervention (such as advertising campaigns or reducing reproductive restrictions) on the sex ratio skew and resulting social problems (see Chapter 9; Ebenstein and Sharygin 2009; Li *et al.* 2000; Tuljapakur *et al.* 1995) in China.

Overall, I aim to show that human society, with its complex institutions, regulations and norms can be understood and perhaps even altered for the better when researchers understand what aspects of humanity and its evolutionary past have allowed us to become masters of social learning. Humans have accumulated enough knowledge to go to the moon and back, build vast cooperative cities, move food and water from areas of plenty to areas of deprivation, irrigate deserts and otherwise alter our environment, at times beyond recognition. Understanding how we alone are capable of generating and maintaining this knowledge over centuries can ultimately help us to understand how culture can lead us, on one hand, to cooperative acts on a scale unprecedented in evolutionary time, and on the other, to the depths of self-made humanitarian disasters. Examining how Darwinian processes at a genetic and cultural level shape humanity is a challenge of increasing importance. We need to know where our culture has come from in order to help determine where it will go next.

SECTION 1:

THE EVOLUTION OF SOCIAL LEARNING AND SOCIAL LEARNING MECHANISMS

SECTION 1, CHAPTER 2:

ROGERS' PARADOX RECAST AND RESOLVED:

POPULATION STRUCTURE AND THE EVOLUTION OF SOCIAL LEARNING STRATEGIES

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INTRODUCTION

Anthropologist Alan Rogers (1988) first pointed out the 'paradox' inherent in the observation that the expected fitness of social learners at equilibrium would be no greater than the average individual fitness in a population of asocial learners. When rare, the fitness of social learners exceeds that of asocial learners but declines with frequency as there are fewer asocial learners producing adaptive information in a changing environment. The population evolves to a mixed evolutionarily stable strategy (*ESS*) where, by definition, the fitness of social learners equals that of asocial learners (Giraldeau *et al*. 2003; Henrich and McElreath 2003). This finding is now commonly known as *Rogers' paradox* (Boyd and Richerson 1985), so called because it contrasts with a commonly held assertion that culture enhances fitness. Although Rogers' result is not inherently paradoxical, it appears to conflict with the observation that social learning underlies the effect of human culture on our ecological success and population growth.

One resolution to this conundrum is to recognise that in a changing environment selection ought to have fashioned in our minds specific evolved rules (Boyd and Richerson 1985), or *social learning strategies* (Laland 2004), that specify the circumstances under which individuals should exploit information from others, and from whom they should learn. Previous theoretical studies have established that the average individual fitness at equilibrium can be enhanced if individuals switch between reliance on asocial and social learning (Boyd and Richerson 1995; Kameda and Nakanishi 2003). For instance, Enquist *et al.* (2007) showed that a strategy of 'critical social learning', where individuals only adopt asocial learning if social learning proves unsatisfactory, out-competes pure asocial and social learning strategies. Boyd and Richerson (1995) also showed that average fitness is higher than that in a population of asocial learners if social learners can improve their learned behaviour so that there is cumulative cultural evolution.

This study extended the above analyses in three important respects. First, it investigates the effects of social and asocial learning in a spatially explicit context. There are several reasons why a spatial framework is appropriate for such analyses (see Chapter 10 for a more thorough discussion). Studies in other contexts have shown that spatial factors can profoundly affect evolutionary outcomes (Nowak and May 1992; Kerr *et al.* 2006; Silver and Di Paolo 2006). Some human cultural phenomena, such as agricultural practices, are physically grounded in space (Durham 1991). Moreover, social learning is now known to be widespread in vertebrates and even some invertebrates (Heyes and Galef Jr. 1996; Leadbeater and Chittka 2007), many of which are sedentary and/or territorial. In such cases, an analysis that recognizes that individuals are often more likely to learn from their near neighbours is appropriate. More generally, by comparing well-mixed and spatially structured populations, the analyses presented here allow us to characterize the extremities of a range of unstructured to structured populations. Learning in a structured population is a special case of bias in social learning, where nearby individuals are preferred as models to distant ones, and in this respect spatially explicit analyses are more generally instructive with respect to the effects of bias (Kameda and Nakanishi 2002).

Second, previous analyses have been generally reliant on deterministic models (in the sense that they ignore random events), although one recent exception is Whitehead and Richerson (2009) who incorporated Brownian noise or ‘red noise’, allowing the environment to vary in large but rare events. However, stochasticity could play an important role in affecting the balance of social and asocial learning, and the nature of the equilibria reached. This analysis utilises a stochastic model that allows individuals to disperse and to learn either locally or globally, thereby allowing us to tease apart the effects of drift and space.

Third, and finally, this analysis investigates the impact of a number of parameters that potentially affect reliance on social and asocial sources of information, but which hitherto have either not been explored, or not been investigated in combination. These parameters include the degree of temporal and spatial variation in the environment, environmental harshness (the extent to which suboptimal behaviour reaps fitness benefits), the number of environmental states (which equates to the number of different ways of performing a suboptimal behaviour), and the relative costs of social and asocial learning.

This analysis shows that spatial structure reinforces Rogers' paradox, because social learning can spread even when it decreases the average fitness of individuals below that of asocial learners. It also shows that there are circumstances under which the strategy of pure, unbiased, social learning increases the average fitness of individuals above that of asocial learners (unbiased here means choosing a model to copy at random). Analysis of the model finds that two conditional strategies, the *critical social learner* (learn asocially only when copying fails) and *conditional social learner* (copy only when asocial learning fails), can both provide solutions to the aforementioned paradoxes, however some conditions where pure social learning out-competes both conditional strategies exist, and thus where the paradox remains. Finally, the relative merits of *critical* and *conditional social learning* across a range of conditions are considered. This extends the findings of Enquist *et al.* (2007) to a stochastic, spatially explicit framework, and across a broader set of conditions.

THE MODEL

The model runs on a square, $x \times x$, toroidal environment, where each cell is occupied by a single individual, such that $n = x^2$ is the population size. Each cell has an associated environmental state which can change over time, and environmental states can vary in space (i.e. between cells). In each time step, all individuals exhibit a behaviour (phenotype), which can change over time, according to the dictates of an evolved learning strategy (their genotype), which is fixed, and governs whether and when individuals learn asocially or socially. The neighbourhood of an individual consists of the eight surrounding cells (the Moore neighbourhood). For mathematical convenience, haploid asexual reproduction is assumed, such that individuals have only one parent.

Environmental variability

Each cell has a value representing its environmental state s, which takes an integer value between 1 and N_s, with adjacent integers representing similar environmental states. A ring structure made it possible for environments to step from N_s to 1, and vice-versa, such that there were no environmental 'end states'. There were two types of environmental variation: (*i*) *temporal only*, where all cells have the same environmental state (s value) but this value can change over time, and (*ii*) *spatio-temporal*, where, in addition, different cells can possess different s values. In the temporal-only condition, all cells switch simultaneously to a new, randomly chosen, value in the range $[1, N_s]$ with probability p_s. In the spatio-temporal condition, environmental variation occurs in two ways – perturbation of patches and single-cell changes. These two types of variation allowed control of the level of spatial auto-correlation while also maintaining a reasonable degree of ecological validity.

Perturbation events convert all the cells in a randomly placed square to a single environmental state in the range [1, N_s], with each state having equal likelihood, and with a single perturbation event in each iteration (a single event per iteration was chosen for computational convenience; increasing the number of perturbations would have the simple effect of increasing the rate of environmental change, a parameter which was varied systematically in the simulations). The size of the perturbed square followed a power law distribution with the side length given by $8R^{-1/6}$ where R is uniform random in the interval [0, 1]. This perturbation regime was chosen for ecological validity as it produces relatively many small perturbations and occasionally large ones, as observed in real-world ecosystems (Langmead 2004). The use of a toroidal environment ensured that all cells had an equal probability of being affected by a perturbation event. Each individual cell subsequently switches state by a single step (i.e. from state *3* to state *2* or *4*) with probability p_s. Two conditions were implemented for these single step changes: cells change either (*i*) towards the average of their neighbours, if that average is different from its current state (spatially correlated condition) or (*ii*) in a random direction (random condition). These conditions produce variation in the level of spatial auto-correlation, measured as the probability of a cell's neighbour being in the same environmental state as itself (henceforth p_n). In the temporal-only condition, $p_n = 1$, while in the spatio-temporal condition, spatially correlated change gives higher values of p_n than random change.

Behaviour, payoff and fitness

Each individual is characterised by behaviour, b, which can take any integer value in the same range as the environment, 1 to N_s, and can change in each model iteration. Each individual's genotype specifies a learning strategy. Two pure strategies were considered, asocial learners (*a*) and random social learners (*s*), as well as two conditional strategies, *conditional social learner* and *critical social learner* (described above). An individual's fitness, *W,* is defined by the difference between the environmental state (*s*) in the cell it occupies and the behaviour it currently shows, minus the cost of the learning strategy it uses:

$$W = h^{-S} - c_{strat} \tag{2.1}$$

where S is the number of steps between b and s implemented as a ring,

$$S_{(b,s)} = \begin{cases} |s-b| & if \quad |s-b| \le \lfloor N_s/2 \rfloor \\ N_s - |s-b| & if \quad |s-b| > \lfloor N_s/2 \rfloor \end{cases},$$

h^{-S} is the payoff associated with being S steps away from the ideal behaviour, and c_{strat} is the cost of the learning strategy (c_a or c_s for the costs of asocial or social learning, respectively, and some additive combination of these in the case of the two conditional strategies). In the case that $c_{strat} > h^{-S}$, W is given a lower bound of zero. The parameter h can be interpreted as the 'harshness' of the environment, as increasing values increment the fitness penalty of behaviour not matching the environment. Higher h values also result in an increasingly non-linear payoff function, while as $h \rightarrow 1$ the payoff function approaches a linear, or 'risk-neutral' form. Note that this incremental fitness structure differs from previous models (e.g. Rogers 1988; Enquist *et al.* 2007), which assumed a fitness payoff for learning the correct behaviour only, with any other behaviour receiving no payoff. In each model iteration, each individual reproduces with probability W, and the resultant offspring always replaces an existing individual such that the population size remains constant across iterations (see *Dispersal* below).

Mutation

In general, offspring carry the same learning strategy as their parent, but at every reproduction event there is a fixed probability, m, of mutation, which results in an offspring with an alternative strategy. This mutation is how new strategies are introduced.

Dispersal

A juvenile developmental period exists during which offspring acquire their parent's behaviour prior to dispersal. This occurs by asocial learning in the same environment as the parent in the case of asocial learners, and by observing the parent in the case of social learners. There are two simulated dispersal conditions. Local dispersal results in offspring replacing a randomly chosen neighbour of the parent. In contrast, global dispersal results in offspring replacing an individual chosen at random from the entire habitat, excluding the parent. In both conditions, individuals are chosen to be replaced irrespective of their fitness and age. Reproduction is synchronous, such that it is not possible for offspring to be replaced in the iteration in which they are born.

Learning

Asocial learners sample their environment and learn the appropriate behaviour, such that $S = 0$, with probability p_{iOK}, and acquire a random behaviour with probability $1–p_{iOK}$. Asocial learners pay a fixed cost c_a irrespective of the learning outcome, such that if $p_{iOK} = 1$ then their fitness is constant at $1–c_a$. Social learners, in contrast, match the behaviour of a randomly chosen demonstrator individual at each iteration, with fixed cost c_s, with demonstrators either chosen from the neighbourhood (local copying) or the entire population (global copying). Consistent with earlier theory (Boyd and Richerson 1985; Rogers 1988) $c_a >> c_s$. Initially the analysis is restricted to these two pure strategies and set $p_{iOK} = 1$, but subsequently the two conditional strategies, *critical social learner* and *conditional social learner* (Enquist *et al.* 2007) are introduced. *Critical social learners* first use social learning, at cost c_s, but if this fails to produce a match to the environment, they then switch to asocial learning, at cost c_a. *Conditional social learners* first try asocial learning, at cost c_a, and only if this fails to produce a match, use social learning at cost c_s. As *conditional social learning* only differs from asocial learning if there is a chance that asocial learning will not work, following Enquist *et al.* (2007) this analysis specifies $0 < p_{iOK} < 1$ when considering the conditional strategies. Thus with probability $1 – p_{iOK}$, asocial learners acquire a random behaviour. For these strategies it is assumed that individuals can know a candidate behaviour does not match the environment, without knowing the exact state of the environment. Individuals using these conditional strategies are forced to accept the final learning outcome they receive. For example, if a *critical social learner* switches to asocial learning it will acquire a random behaviour with probability p_{iOK} and is forced to accept that behaviour even if it returns a lower fitness than the behaviour it originally learned socially and rejected.

Spatial population structure

This analysis principally considered two conditions, termed *local* and *global*. In the *local* condition, both dispersal and copying were local – offspring disperse only to the neighbourhood and social learners copy only neighbours. In the *global* condition, dispersal and copying were with respect to the entire population, as described above. These two conditions represent a maximum and minimum level of population structure within the model. Intermediate levels can be represented by simulations in which only learning is local (*local learning*) or only dispersal is local (*local dispersal*) and both these cases were considered in the initial exploration of spatial effects, however, the latter condition (*local dispersal* with *global learning*) is biologically rather less plausible than the other three. In this way the effect of population structure could be explored without altering other conditions.

Demography

In the general model, increasing or decreasing average individual fitness affects only the rate of population turnover, as the model specifies a fixed population size. While this assumption has utility in helping to understand the relative efficacy of alternative learning strategies, it does not allow the model to investigate the demographic consequences of changes in individual fitness. Therefore a variant of the model was constructed that did allow for demographic effects, by making the simple assumption that the probability of any individual surviving to the next iteration ($p_{survive}$) is related to their fitness by the equation $p_{survive} = p_{surviveMin} + (1 - p_{surviveMin})W$, where $p_{surviveMin}$ is a parameter that defines the minimum probability an individual survives a model iteration and thus sets the strength of viability selection in the model. Thus it is possible for the population to vary in size between zero (extinction) and the maximum n, the latter representing the carrying capacity of the environment. In this case empty cells provide no model for social learners to copy, but are no more likely to be occupied by new offspring than cells that are already occupied.

Simulation details

Each model iteration consisted of the following sequence of events: learning, followed by reproduction and dispersal, and then environmental change. For most simulations x is set at $x = 80$, giving a population size, n, of 6400 individuals. This value of n was chosen so as to be broadly representative of human populations (6400 is close to the median for horticultural and herding societies, and intermediate between hunter-gatherer and agrarian societies, Lenski 1974). Mutation was set at $m = 0.0008$, equating to five individuals per complete generation when $n = 6400$. While this is obviously high relative to natural rates of mutation in eukaryotes, reducing this rate does not qualitatively affect the outcomes, and the higher rate offers significant computational advantages in terms of time to equilibrium. All individuals were behaviourally naïve at the start of each simulation (i.e. $b = 0$). Below the results of sensitivity analyses investigating the extent to which the conclusions are robust across a range of biologically plausible values of n and m are discussed.

The effects of spatial variation in environmental conditions were explored by producing three spatial auto-correlation conditions, where the auto-correlation is expressed as the probability (p_n) that two randomly chosen but neighbouring cells have the same environmental state (which is effectively the auto-correlation but with a ‘spatial lag’ of one cell). The three conditions were $p_n = 1$ (no spatial variation at all), $p_n \approx 0.44$ and $p_n \approx 0.2$. The latter two values are approximate as they result from stochastic simulation runs, thus the actual realised value in each simulation varied around these values; the actual values were recorded during simulation runs. These simulations were run with $N_s = 10$, and *local* learning and dispersal, in order to explore conditions where Rogers’ paradox may not exist. Environmental harshness (h) was in the range $1.1 \leq h \leq 5$.

Simulations were run for 2000 iterations, with 20 replications per parameter value, and from each simulation the mean proportion of each strategy over the final 250 iterations of the run was recorded. Sensitivity analyses established that either increasing the number of iterations over which each simulation was run to 10,000, or increasing the number of runs per parameter set to 200, produced no change in the results.

First the performance of a pure unbiased social learning strategy invading a population of pure asocial learners was investigated and, unless otherwise specified, it was assumed that $p_s = 0.1$, $c_s = 0$, $p_{iOK} = 1$, with c_a increasing from 0.01 to 0.7 in steps of 0.01. Subsequently the evolution of conditional strategies, again starting from a population of asocial learners was examined. All four genotypes (the two pure and two conditional strategies) were examined simultaneously, by considering the dynamics of a population of asocial learners capable of mutating to the other three genotypes. As *conditional social learning* only makes sense when there is a possibility of individual learning not working (i.e. $p_{iOK} < 1$), this comparison was made with $p_{iOK} = 0.5$. These analyses introduced spatial variation in the environment by setting $p_n \approx 0.44$.

RESULTS

Analysis of pure strategies

Effect of local dispersal and learning

First, the relative performance of the pure asocial and social learning strategies was examined in a spatially homogenous environment ($p_n = 1$). Note that the *global* condition produced a qualitatively good fit to analytical expectations (Rogers 1988; Enquist *et al.* 2007) with respect to the magnitude of c_a at which social learners will invade, the resultant average final frequency of social learners, and the mean individual fitness in the population at run termination (Figure 2.1). Similar to Rogers' (1988) model, in the global condition the mean individual fitness approximates that expected in a population of entirely asocial learners, although it is marginally higher than expected for large c_a (Figure 2.1b), whilst social learning frequencies were slightly lower than the analytical prediction (Figure 2.1a). These discrepancies can be attributed to minor differences in the assumptions of this model compared with the cited analytical treatments (see discussion in this chapter).

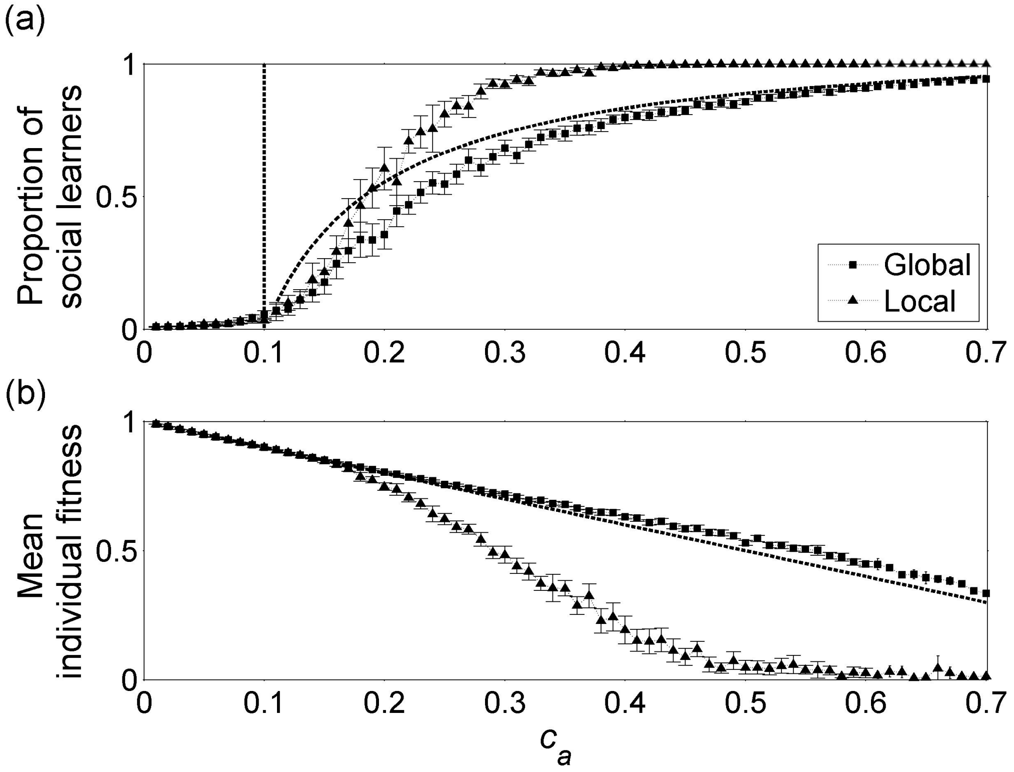

Figure 2.1. The effect of spatial population structure: *global* versus *local* dispersal and learning, showing (a) the proportion of social learners, and (b) mean individual fitness, at run termination, plotted against the cost of asocial learning (c_a). In both, $N_s = 1000$, $h = 2$, and $p_n = 1$. Points are means from 20 runs ± 95% confidence intervals. The vertical dashed line in the upper panel shows where analytical models (Enquist *et al.* 2007) predict non-zero equilibrium levels of social learners, with the curved dashed line giving the analytical prediction for the frequency of the social learning strategy. The dashed line in the lower panel shows the expected mean individual fitness in a population of asocial learners only.

Local dispersal and learning typically generates higher average final frequencies of social learners than *global* dispersal and learning, particularly for larger values of c_a, and can lead to social learners reaching effective fixation (with an expected frequency of $1 - m$). Moreover, under local conditions the mean individual fitness in the population is predicted to be less than that expected for a population consisting of asocial learners, under conditions where the frequency of social learners exceeds the analytical prediction. Thus, when population structure is imposed, not only does social learning invade and fail to increase mean individual fitness, it may actually invade to fixation and reduce fitness relative to a population containing only asocial learners.

The observation that social learning spreads to near fixation in spite of the fact that it reduces average individual fitness introduces a new dimension to the debate surrounding Rogers' paradox. This observation can be explained by comparing the fitness of social learners that have at least one asocial learner in their neighbourhood with those that do not (Figure 2.2). When learning and dispersal are local, social learners with at least one asocial learner in their neighbourhood have greater fitness than both social learners with no asocial learner in their neighbourhood (Figure 2.2a) and asocial learners (Figure 2.2b). This creates an edge effect in the contact zones between genotypes, and since social learners have greater fitness in these zones they can continue to increase in frequency even when, on average, social learners have lower fitness than asocial learners. Asocial learners cannot invade the regions dominated by social learners because their social learning neighbours will have a higher fitness immediately after an asocial learner mutates into their midst.

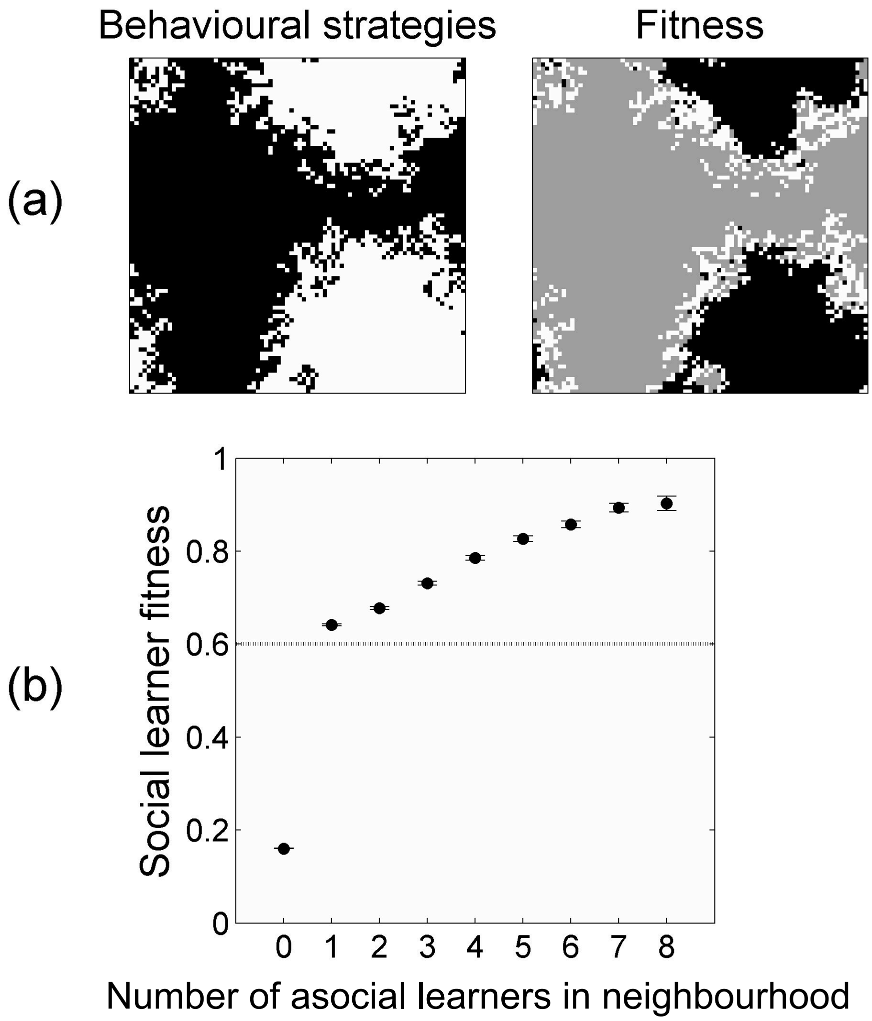

Figure 2.2. (a) Snapshot of a running simulation with *local* learning and dispersal and a spatially uniform environment, taken within a few iterations of an environmental state change. Left panel shows spatial distribution of learning strategies (black = asocial learner, white = social learner). Right panel shows the fitness of each individual; the lighter the cell, the higher the fitness value. Asocial learners have a fixed fitness (1-c_a), which appears as grey. Social learners in the border regions have the highest fitness (appearing white in the right panel) even though most of the social learners have much lower fitness (appearing black). (b) Mean fitness of social learners plotted against the number of asocial learners in their neighbourhood over the same simulation (error bars show 95% CI). Dashed line shows fitness of asocial learners.

In *local learning* and *local dispersal* conditions, where only one of learning or dispersal were local, local learning alone produced identical results to *global* learning and dispersal. In contrast, *local dispersal* with global learning gave intermediate results, where some fixation of social learning was observed, but in a restricted parameter range compared to the *global* case.

Thus far in the analysis, increasing or decreasing average individual fitness affects only the rate of population turnover because the model specifies a fixed population size. While helping to understand the relative efficacy of various learning strategies, this feature means it is not straightforward to understand the demographic consequences of changes in average individual fitness. Therefore the above simulations were run with a modified version of the model which allowed for demographic effects by making the simple assumption that the probability of any individual surviving to the next iteration is related to their fitness. When this model was run under the *local* conditions specified above, analysis obtained identical results in terms of social learner frequency and mean individual fitness, but with the confirmation that reduced mean individual fitness results in decreased population size, culminating in extinction when the average probability of reproduction approaches zero ($W \to 0$; Figure 2.3). When viability selection was relatively weak (i.e. the minimum survival probability, $p_{surviveMin}$, was close to 1), there was a significant portion of the parameter space where social learning would approach fixation, resulting in a stable population with reduced size compared to one containing only asocial learners. Stronger viability selection ($p_{surviveMin} << 1$) under local conditions does not prevent the spread of social learners in spite of the fact that they reduce mean individual fitness to sufficiently high frequency that the population goes extinct (Figure 2.3). These results did not change whether the simulations started with populations size set to 1 (i.e. at carrying capacity) or 0.5 (half carrying capacity).

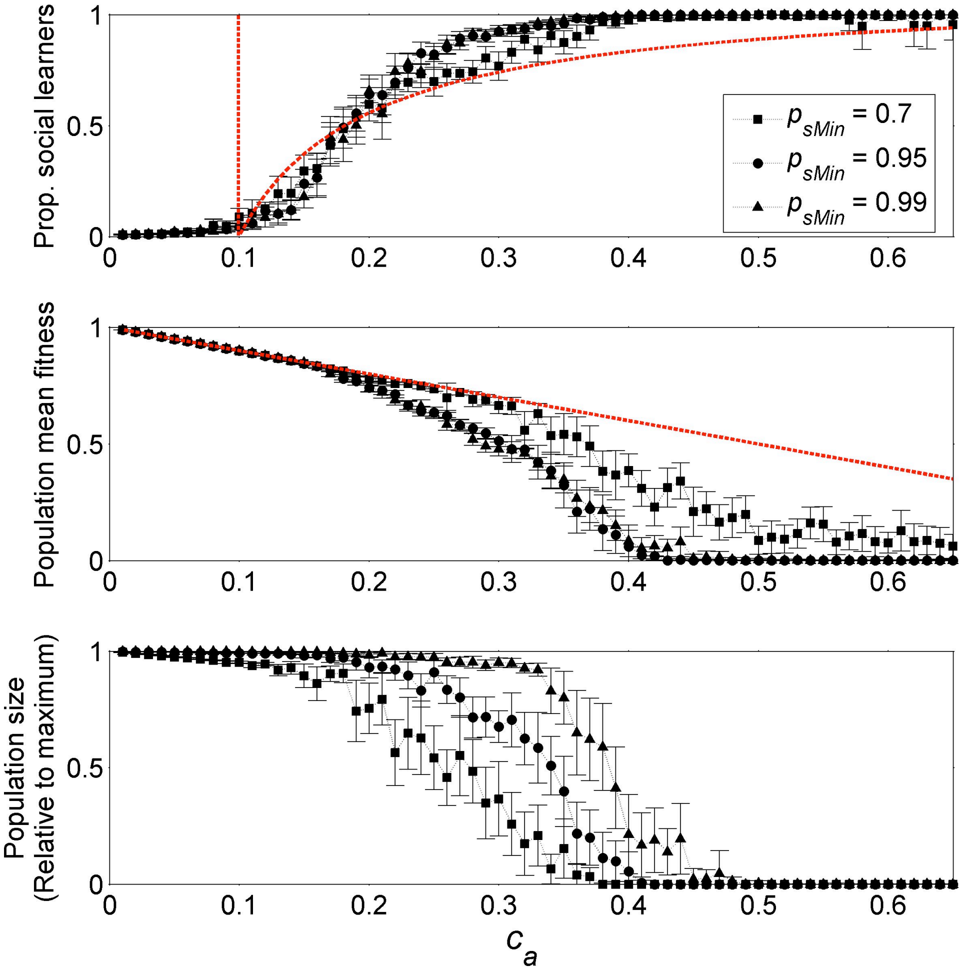

Figure 2.3. Demographic consequences of social learner invasion. Results are from simulations run under identical conditions to the *local* condition in Figure 2.1 with the exception that the probability an individual survives a model iteration is proportional to its fitness. Top panel shows the proportion of social learners, middle mean individual fitness, and bottom panel population size at run termination, plotted against the cost of asocial learning (c_a). Points are means from 20 runs ± 95% confidence intervals, and the dashed lines in the top and middle panels are identical to those in Figure 2.1.

The above findings are generally robust across values of N_s (the number of possible environmental states) between 10 and 1000 and values of h (controlling the harshness of the penalty for sub-optimal behaviour) from 1.1 to 5, with one important exception. For small N_s (e.g. $N_s = 10$), and in the *local* condition only, it was seen that for large c_a (e.g. $c_a \geq \sim 0.5$), the mean fitness of individuals in the population was elevated compared to that expected for a population of only asocial learners (Figure 2.4a).

Since under these conditions random copying does increase mean individual fitness, this represents a set of conditions under which Rogers' original paradox does not exist. This fitness advantage of social over asocial learning is due to the assumption that offspring acquire the behaviour of their parents during maturation – if offspring are assigned a random behaviour at birth, high frequencies of social learners do not increase fitness (Figure 2.4a). Note that the acquisition of parental behaviour has no direct effect on offspring fitness, because offspring must undergo an independent learning round after dispersal before selection occurs. It does however increase the pool of potential models for social learners to copy. Since these models are offspring of individuals with relatively high fitness, on average, they will be performing locally adaptive behaviour patterns, making them available for social learners in the neighbourhood to copy. Thus, acquisition of parental behaviour provides indirect fitness benefits to social learners. As these effects are reliant on the learning of locally adaptive behaviour, low levels of spatial autocorrelation in the environment reduce the magnitude of this fitness increment (see below).

The simulations reported here had the same mutation rate ($m = 0.0008$) and population size ($n = 6400$). Exploration of the effects of varying these parameters showed that the results were largely robust to such variation. Note that because m is a rate, changing the population size (n) alters the absolute number of mutations per generation, and therefore these two parameters are intimately related. Changes in m or n have an intuitive effect on genotype frequencies: as expected, increasing mutation rate (or decreasing population size) increases the frequency of the less common genotype, and vice-versa. Accordingly, when social learning is common, mutation will tend to introduce asocial learners, and since the latter acquire adaptive behaviour this means that the amount of correct information entering the population each generation co-varies with the mutation rate. Increased mutation rates (or reduced population sizes) are therefore associated with increases in the mean fitness of individuals in the population. The reverse holds when the asocial learners dominate. In contrast, decreased mutation rates accentuate the fitness reductions associated with the *local* condition (e.g. Figure 2.1), because new, correct, information enters the population less frequently.

Spatial variation in the environment

The level of spatial auto-correlation in the environment greatly affected the frequency of social learners in the population (Figure 2.4a). Typically, spatial environmental variation reduces the benefits of social learning, since it reduces the probability that copied individuals will have experienced the same environment as the copier. This means that social learning requires higher costs of asocial learning to invade a spatially variable environment, compared with a uniform one. When dispersal and learning are *global,* small values of p_n mean that social learning never becomes established. However, local learning partly negates these effects. In the local condition, at intermediate levels of spatial autocorrelation ($p_n \approx 0.44$) social learning can only become established at higher levels of c_a than the $p_n = 1$ case, although the subsequent transition to fixation occurs over a smaller range of c_a values. This effect is exaggerated at $p_n \approx 0.2$, with social learners unable to invade until c_a is very large, since social learning has to be considerably cheaper than asocial if it is to have an advantage, even when copying an asocial learner directly only returns good information 20% of the time. Provided spatial autocorrelation is sufficiently high, local learning results in an increase in mean individual fitness above that expected for asocial learners, even when social learning reaches near fixation. This establishes further conditions for which Rogers' paradox does not apply. Conversely, low spatial autocorrelation leaves mean individual fitness at or near that expected for a purely asocial learning population, even with *local* learning.

In contrast to uniform environments, changes in environmental harshness (h) have major effects on the frequency of social learning in spatially varying environments (Figure 2.4b). Increasing h has the effect of reducing the fitness payoff to social learners performing sub-optimal behaviour, the frequency of which increases with spatial variation. However small N_s values ameliorate the impact of increased h, since proportionally more behaviour patterns will reap higher fitness dividends. This also means that lower values of h result in an escape from Rogers' paradox at relatively low levels of c_a, when N_s is low.

Predicting when social learning will invade

Here an analytical approximation for the conditions under which a pure social learning strategy will invade a population of asocial learners under local learning conditions is derived. Near the asocial learning fixation boundary, the social learning genotype will increase when its expected fitness (W_S) exceeds $1–c_a$, which is the constant fitness of asocial learners (assuming $p_{iOK} = 1$). In the invasion condition of a single social learner mutating into a neighbourhood of asocial learners, the probability of that social learner copying correct behaviour from a neighbour is given by the probability that the neighbouring cell has the same environmental state multiplied by the probability that the neighbouring cell has not changed state in the iteration since its occupant learned the correct behaviour. This can be written as $p_n(1–p_c)$, where p_c is the probability of a cell changing environmental state per iteration. When the environment is spatially uniform, p_c equals the model parameter p_s, and when it is not,

$p_c \approx p_s+80/n$ (the second term being the probability of a cell being included in a perturbation event of area $(8R^{-1/6})^2$ where the expectation of R is 0.5). When learning is correct, then the payoff is 1. When learning is not correct, with probability $1-p_n(1-p_c)$, then the expected payoff $\boldsymbol{E}_s$ approximates a weighted average of the payoffs when S (from Equation 2.1) is greater than zero, as it must be when environment and behaviour do not match. Here the weights are the probabilities of neighbouring cells being a given number of environmental state steps apart. These considerations allow us to derive an expression for the expected fitness of an invading social learner (W_S) surrounded by asocial learners, or

$$W_s = p_n(1-p_c)+(1-p_n(1-p_c))E_s - c_s\,, \qquad (2.2)$$

As successful invasion requires that $W_S > 1 - c_a$, the condition for invasion can be written as

$$c_a > 1 - p_n\left(1-p_c\right) - \left(1-p_n\left(1-p_c\right)\right)E_s + c_s\,, \qquad (2.3)$$

where

$$\boldsymbol{E}_s = \frac{\sum_{i=1}^{\lfloor N_s/2 \rfloor} w_i h^{-i}}{\sum_{i=1}^{\lfloor N_s/2 \rfloor} w_i}\,,$$

and **w** is a vector of the probabilities that two neighbouring cells will be $[1,2,\ldots,\lfloor N_s/2 \rfloor]$ environmental state steps apart. Because of the stochastic nature of the simulations and the complex spatial variation that resulted, **w** must be calculated directly from the simulation runs. Note however that any behaviour-payoff function can be used to calculate $\boldsymbol{E}_s$ for Equation 2.2 provided it generates an expectation when behaviour is sub-optimal.

The predictions generated by this inequality conform reasonably well to the simulations (Figure 2.4). Note that when there is no spatial variation ($p_n = 1$), no cost to social learning ($c_s = 0$), and an infinite sequence of possible environmental states ($N_s = \infty$), as posited by Rogers (1988) and Enquist *et al.* (2007), then $\boldsymbol{E}_s = 0$, and (2.2) simplifies to $c_a > p_c$, as in their models. Equation 2.3 specifies that whether a strategy of pure social learning will invade depends not only on the relative costs of social and asocial learning and the rate of environmental variation, but also on the level of spatial auto-correlation in the environment and the expected payoff of choosing a sub-optimal behaviour at random.

Analysis of conditional strategies.

Here the merits of two conditional strategies, *conditional social learning* (where asocial learning is attempted first followed by social learning if asocial learning fails) and *critical social learning* (where social learning is attempted first followed by asocial learning if a correct result is not obtained) are considered. In order to directly compare the model presented here to the analytical results of Enquist *et al.* (2007), $p_n = 1$. This analysis found that *critical social learning* was able to both invade a population of pure asocial learners and increase individual mean fitness under the same conditions predicted by Enquist *et al.* (2007). *Local* learning and dispersal made very little difference to this pattern of results. All four genotypes (the two pure and two conditional strategies) were also examined simultaneously by considering the dynamics of a population of asocial learners capable of mutating to any the other three genotypes. When $p_{iOK} < 1$, the expected fitness of asocial learners (W_a) is given by

$$W_a = p_{iOK} + (1 - p_{iOK})\boldsymbol{E}_a - c_a \qquad (2.4)$$

where $\boldsymbol{E}_a$ is the expected payoff when asocial learning fails (i.e. the expected payoff of a randomly chosen behaviour), given by

$$\boldsymbol{E}_a = \frac{\sum_{i=1}^{Ns} h^{-S_{(1,i)}}}{N_s}.$$

Again, the results are virtually identical to Enquist *et al.*'s (2007) consideration of three strategies (asocial plus the two conditional strategies) under similar conditions (Figure 2.5a). Pure social learning never attained frequencies above the mutation rate in any of the simulations, which is explained by the observation that social learners never had fitness higher than either asocial learning or either conditional strategy when surrounded by those strategies (Figure 2.6). Results for the *local* and *global* conditions were comparable.

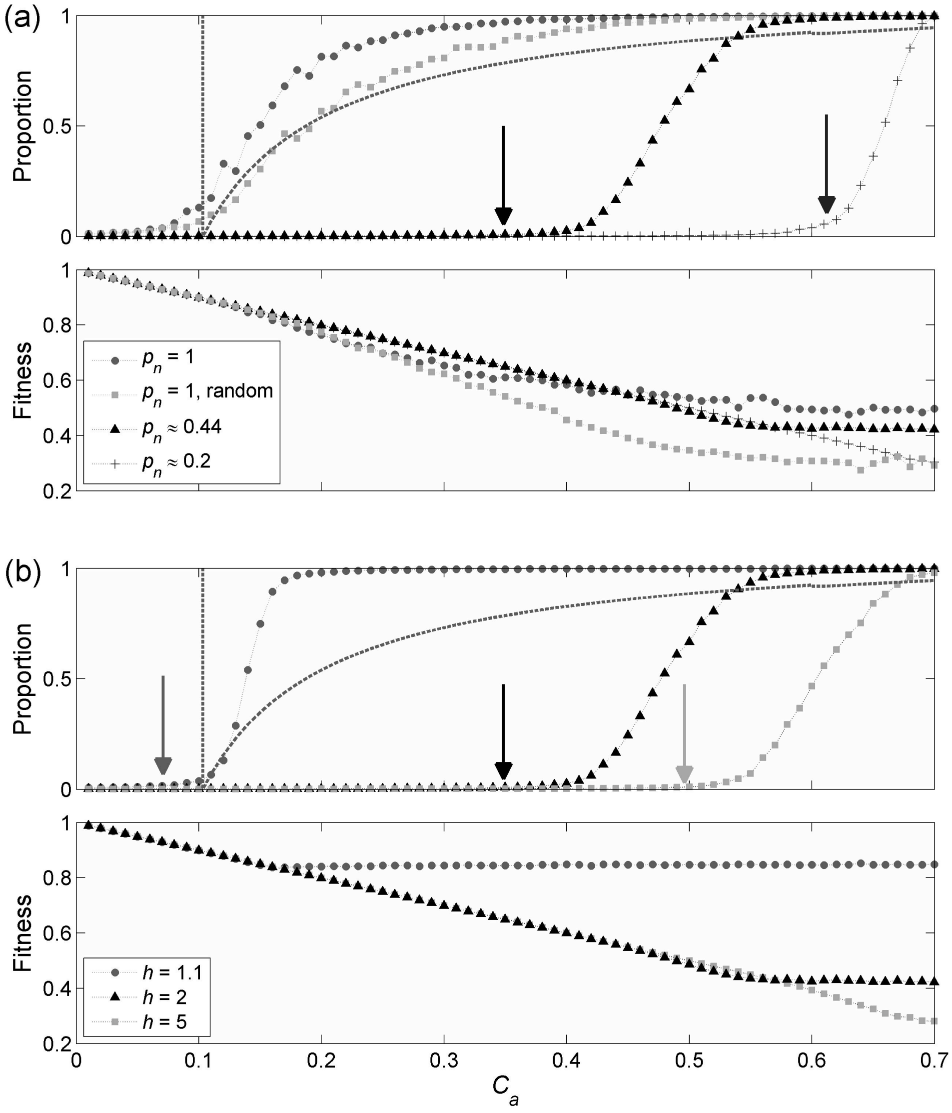

Figure 2.4. The effect of (*a*) spatial variation in the environment, and (*b*) the harshness of the fitness penalty for sub-optimal behaviour, on the proportion of social learners and mean individual fitness in simulated populations. Spatial variation is represented by the parameter p_n, the probability that two neighbouring cells have the same environmental state, and harshness by the parameter h (see Equation 2.1). In all cases learning and dispersal are local, and if not otherwise specified $N_s = 10$, $h = 2$, and $p_n \approx 0.44$. Note that the data labelled 'random' in (a) come from simulations where there was no acquisition of parent's behaviour by offspring. Points are means from 20 runs, error bars are omitted for clarity. Dashed lines are as in Figure 2.1. Arrows indicate where an invading social learner has equal fitness to surrounding asocial learners according to Equation 2.3. In the case $p_n \approx 0.2$ in (a), note that when c_a is high (>0.5), fitness, reproductive rate, and thus selection strength is low, such that drift effects are able to maintain low levels of social learners in the population even when their fitness is slightly lower than asocial learners.

Conditional and critical social learning in spatially heterogeneous environments

However, the results of this model differ markedly from earlier theory (Rogers 1988; Enquist *et al.* 2007) when spatial variation was introduced to the environment. In the *local* condition, it was found that the parameter space where *conditional social learning* was favoured over *critical social learning* was significantly expanded, such that *critical social learning* only dominated at higher levels of c_a (Figure 2.5b-d). In spatially heterogeneous environments, social learning is less effective than in uniform environments, since individuals are more likely to pick up inappropriate information from others. (This is illustrated by the fitness of social learners in Figure 2.6). This has the effect of decreasing the probability that *critical social learners* will find an optimum behaviour through social learning, which they attempt first, and consequently increases the likelihood that they will also pay the cost of asocial learning. Figure 2.6 illustrates how the fitness advantage of *critical social learning* over *conditional social learners* observed in a spatially homogeneous environment is reversed in a spatially heterogeneous environment, since the comparative ineffectiveness of social learning means that *critical social learners* more frequently pay the cost of both forms of learning than do the conditional social learners.

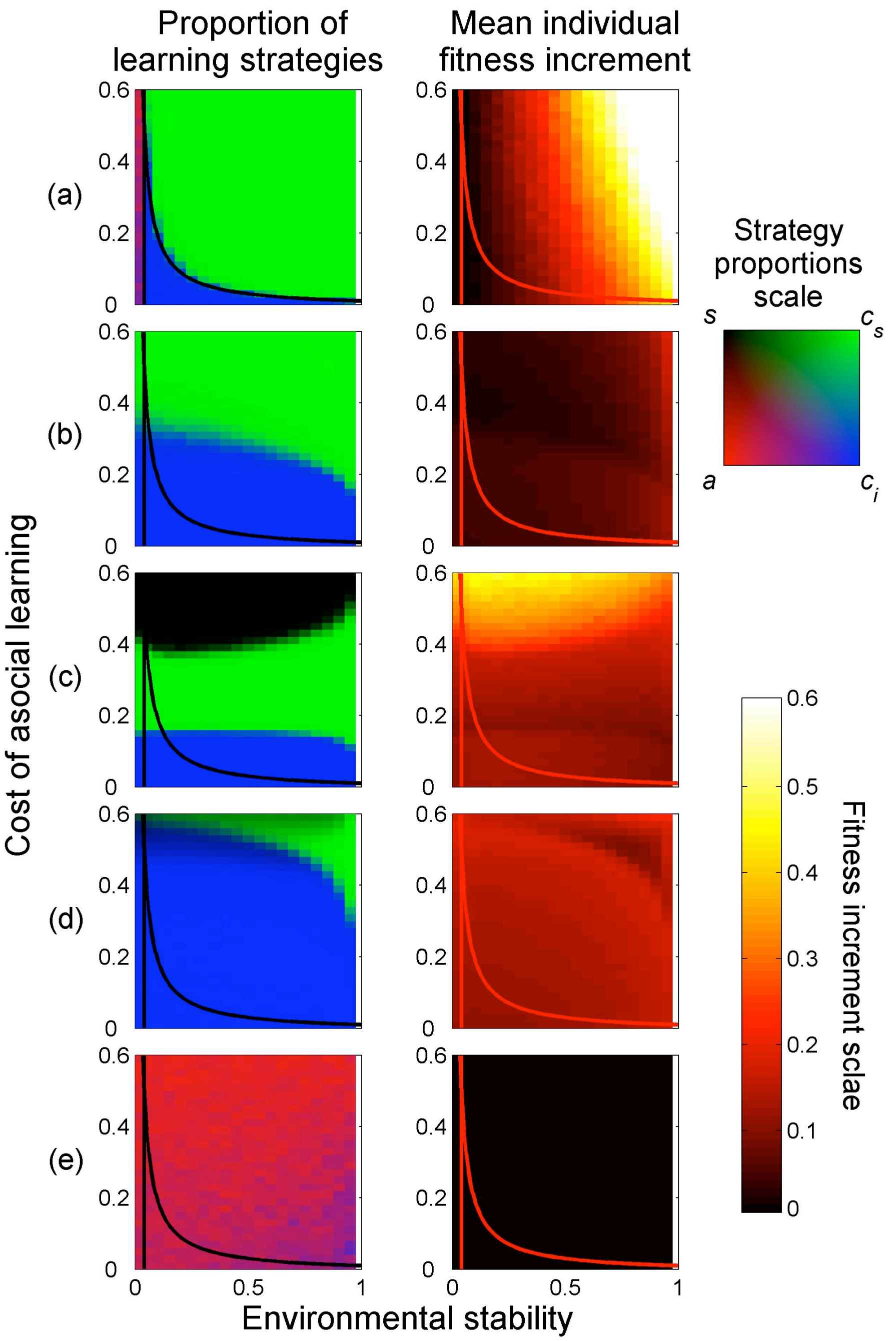

Figure 2.5. Frequencies of asocial (*a*, red), social (*s*, black), *critical social* (c_s, green) and *conditional social* (c_i, blue) learning strategies (left panel), and population fitness increment over that expected of a purely asocial learning population (right panel), with the cost of asocial learning plotted against environmental stability. Solid lines are estimates of the analytical predictions of Enquist *et al.* (2007) for a perfectly mixed population. Unless otherwise specified $N_s = 1000$, $h = 2$, $p_{iOK} = 0.5$, $c_s = 0.02$, and learning and dispersal are *local*. (*a*) No spatial variation, $p_n = 1$. (*b*) Effect of spatial environmental variation; $p_n \approx 0.44$. (*c*) Effect of reducing N_s; $N_s = 10$ and $p_n \approx 0.44$. (d) Effect of reducing *h*; $h = 1.1$ and $p_n \approx 0.44$. (*e*) Effect of *global* learning and dispersal, in a spatially variable environment, $p_n \approx 0.44$.

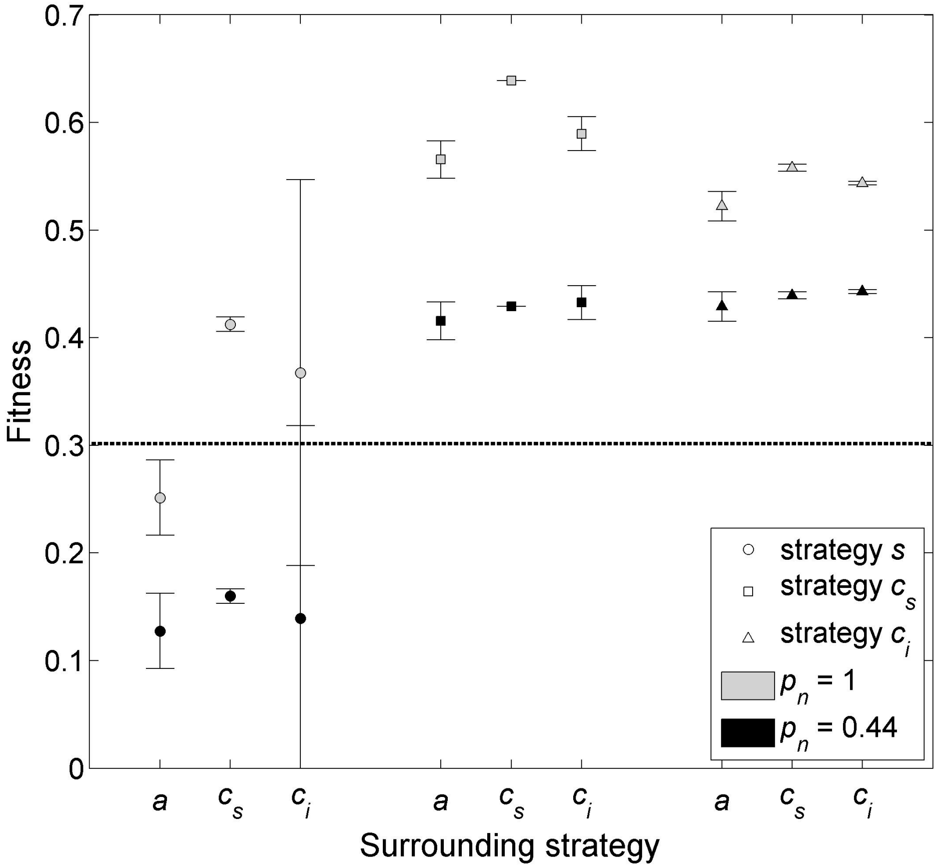

Figure 2.6. Mean fitness of social learners (s), *critical social learners* (c_s) and *conditional social learners* (c_i) when surrounded entirely by individuals of other strategies, in simulations under the same conditions as those in Figure 2.5a (spatially uniform environment, P_n = 1) and 2.5b (spatially heterogeneous environment, P_n = 0.44), with c_a = 0.2 and p_c = 0.5. Errorbars show standard errors of the means. No data are shown for any strategy surrounded entirely by social learners, as pure social learners never attained sufficient frequency in these simulations to completely surround any cell. Dashed line shows fitness of asocial learners calculated using Equation 2.4.

In the *global* condition, in general, no strategy involving social learning reached high frequency, except in the region where asocial learning is relatively cheap and the environment is highly stable (Figure 2.5e). Under these conditions, *conditional social learning* can reach relatively high frequency, but even then any increase in mean individual fitness is negligible. Surprisingly, this leads to the counter-intuitive prediction that a social learning strategy will be favoured when asocial learning is cheap (see the discussion in this chapter).

Once again, these qualitative findings are robust to variations in both the number of environmental states (N_s) and the harshness of the environment (h). Note, however, that where N_s is small and c_a is high, there are broad circumstances under which the pure strategy of random social learning is favoured over both conditional strategies (e.g. Figure 2.5c, where N_s = 10). Here the high probability of acquiring high fitness behaviour by chance renders the additional cost of sometimes, or always paying the cost of asocial learning, unprofitable. Reducing the harshness of the environment increases the range of parameter space over which the *conditional social learning* strategy out-competes the *critical social learning* strategy (Figure 2.5d).

These results can be better understood with reference to expressions for the expected fitness of the conditional strategies, W_{crit} and W_{cond} for *critical social learner* and *conditional social learner*, respectively, given by

$$W_{crit} = p_{sOK} + (1 - p_{sOK})(p_{iOK} + (1 - p_{iOK})\boldsymbol{E}_a) - (c_s + (1 - p_{sOK})c_a) \qquad (2.5)$$

and

$$W_{cond} = p_{iOK} + (1 - p_{iOK})(p_{sOK} + (1 - p_{sOK})\boldsymbol{E}_s) - (c_a + (1 - p_{iOK})c_s), \qquad (2.6)$$

where the term p_{sOK} represents the probability that social learning returns the optimum behaviour. *Critical social learners* outcompete *conditional social learners* when W_{crit} > W_{cond}, which simplifies to

$$\boldsymbol{E}_a(1 - p_{iOK})(1 - p_{sOK}) + c_a p_{sOK} > \boldsymbol{E}_s(1 - p_{iOK})(1 - p_{sOK}) + c_s p_{iOK}\,.$$

By denoting $\boldsymbol{E}_s = \boldsymbol{E}_a + \alpha$, we can simplify this expression further to give

$$c_a p_{sOK} - c_s p_{iOK} > \alpha(1 - p_{iOK})(1 - p_{sOK})\,. \tag{2.7}$$

This inequality illustrates how high values of the cost of asocial learning (c_a) and of the probability that social learning returns optimal behaviour (p_{sOK}) will favour *critical social learning*. Environmental homogeneity (high p_n, low p_c) typically generates high values of p_{sOK}, since it makes it more likely that the copied individual will exhibit the correct behaviour for the observer, giving critical social learners the advantage. Conversely, environmental heterogeneity (low p_n, high p_c) reduces the efficacy of social learning (reduces p_{sOK}), allowing *conditional social learners* to invade. The inequality also shows how the greater the magnitude of the expected payoff from sub-optimal copied behaviour over randomly chosen behaviour (a), the more likely that *conditional social learning* invades. Any such increase in α will be affected by environmental autocorrelation and also the parameter h.

DISCUSSION

This analysis has explored the evolution of different forms of learning using a spatially explicit stochastic model that incorporates a number of factors that have previously been absent or rare in theoretical literature on the evolution of social learning. This model was first validated by comparison to earlier analytical treatments (Rogers 1988; Enquist *et al.* 2007) and it was seen to behave comparably. There were nonetheless small, but notable, discrepancies in some cases. For example in the *global* condition shown in Figure 2.1, frequencies of social learning were lower, and mean individual fitness was slightly higher, than the analytical prediction. These minor differences can be attributed to two factors.

Firstly, in the model of Enquist *et al.* (2007), cultural evolution (the spread of information by social learning) and genetic evolution (the change in strategy genotypes over time) were strictly separated, largely for reasons of analytical tractability, under the assumption that the former was rapid compared to the latter and thus likely to reach equilibrium before the next biological generation. In contrast, these processes occur concurrently in the models presented here, such that selection could act against social learners to whom correct information had not yet diffused following environmental change, disfavouring social learners relative to the analytical case.

Secondly, the models here assume that offspring acquire the same behaviour as their parent, either directly because of vertical cultural transmission, or indirectly because through asocial learning each is exposed to the same environmental contingencies. Given that those parents with correct behaviour are disproportionately more likely to reproduce, this factor would tend to increase mean individual fitness slightly. While vertical transmission does not directly increment offspring fitness, it increases the pool of potential ‘demonstrators’ performing high-fitness behaviour patterns that are available to be copied, and hence provides peripheral fitness benefits to social learners. Despite this, the behaviour of these models is qualitatively similar to those of Rogers (1988) and Enquist *et al.* (2007), which lends confidence that the extensions into analytically intractable contexts are well-founded in existing theory.

The most striking finding here is that, when learning and dispersal are confined to local neighbourhoods, social learning can invade to effective fixation and yet result in a population with lower mean individual fitness than would be expected with asocial learning alone. This can be explained by examining the fitness of different segments of the social learner population as the simulation runs. The most useful comparison is between those social learners that have at least one asocial learner in their neighbourhood and those that do not. In the condition where learning and dispersal are global, both these sub-populations have identical fitness. However, when learning and dispersal are local, social learners with at least one asocial learner in their neighbourhood have greater fitness than both other social learners, and those asocial learners that have at least one social learner in their neighbourhood. In other words, there is an edge effect wherever social learners are in contact with asocial learners (social learners can acquire useful information from nearby asocial learners at low cost) and as dispersal is local, then the strategies can only replace each other in these edge zones. Since the social learning genotype has greater fitness in these contact zones, social learners increase in frequency even though on average they have lower fitness than asocial learners (Figure 2.2). This perpetuates even though mutations can give rise to asocial learners within the social learner population because as soon as an asocial learner arises through mutation, the social learners surrounding it jump in fitness as they now have a useful source of information available, generating selection against the mutants. In contrast, social learners surrounded only by other social learners are isolated from such useful information, and are forced to become part of an information cascade relying on increasingly out-dated information with well understood detrimental consequences when the environment changes (Bikhchandani *et al.* 1992; Giraldeau *et al.* 2003). By this process, the ability of the population to track a changing environment is lost, so mean individual fitness falls almost to zero.

The fitness associated with differential learning strategies in the model can be considered in two ways. The first is to consider the fitness associated with learning to be just one component of an individual's fitness, and hence having a mean individual fitness of zero need not correspond to population shrinkage if a baseline fitness level is assumed that maintains the population. The second is to consider the fitness in these models as representing the entire fitness of the individuals concerned. Under this interpretation, the way this analyses artificially holds population size constant can make it difficult to interpret the results in term of demographic consequences. The extension to incorporate viability selection (Figure 2.3) helps in this regard by showing that reductions in average individual fitness due to high levels of social learning in a population do indeed reduce population size, and can lead to extinction. Here, the results are very similar to those obtained by Whitehead and Richerson (2009). While the risks associated with over-reliance on social learning producing information cascades are well understood (Bikhchandani *et al.* 1992; Giraldeau *et al.* 2003), the role that population structure could play in producing cascade-like effects, and their population level evolutionary effects, has not been previously appreciated.

While no real-world population would be as rigidly structured as those in these simulations, the *local* condition in the analysis represents one bound of the spectrum of possible structural constraints, with the equally unrealistic perfect mixing assumed by analytical models (and the *global* condition in this model) representing the other. Real populations would be found somewhere between these two bounds, which means that any invasion of a pure strategy of social learning may reduce fitness. It is not hard to find examples of population structure with regard to information flow. One example is the Landga people of New Guinea, where 'craftsmen report that, because of the great value of the skill [of stone adze construction], they will instruct only close relatives' (Stout 2002). Futhermore, spatial structure can be thought of as equivalent to any social learning bias which results in copying from only a select few behavioural models (Kameda and Nakanishi 2002). Thus this analysis suggests that Rogers' paradox is even stronger than originally thought; pure social learning doesn't just fail to increase fitness, it may even frequently reduce it.

This model, however, can also show some conditions where this paradox need not apply. Under the specified behaviour and payoff structure, increasing the number of environmental states effectively increases the number of ways an individual can generate sub-optimal solutions and thus have low relative fitness. The parameter h, which can be interpreted as representing the 'harshness' of a particular environment, sets the size of the relative fitness increment (ΔW) available to organisms that perform the correct behaviour compared with alternatives (as $h \rightarrow 1$, then $\Delta W \rightarrow 0$). Intuitively, it makes sense that as the fitness cost of acquiring a sub-optimal behaviour through copying decreases then that cost will become less significant relative to the cost of asocial learning, and so social learners will be favoured. This pattern was observed in those simulations where h and N_s were manipulated. Under conditions when h and/or N_s are low and c_a sufficiently high, random social learning can increase the mean fitness of individuals. These conditions represent relatively benign ecological contexts, where almost any realistic behaviour leads to some fitness benefit.

The analysis of conditional strategies presented here endorses the conclusions of Enquist *et al.* (2007) that the *critical social learner* and *conditional social learner* strategies resolve Rogers' paradox. Enquist *et al.* suggested that *critical social learners* out-compete *conditional social learners* over a broad area of the parameter space defined by the cost of asocial learning, c_a, and environmental stability $(1 - p_c)$, and under the conditions they explored, the models here generate the same findings (Figure 2.5a). However, the introduction of a spatially varying environment in simulations significantly alters these conclusions (Figure 2.5b-e) by revealing conditions under which the *conditional social learning* strategy is favoured over the *critical social learning* strategy. This analysis suggests that the cost of asocial learning is the more important factor in determining the switch between *conditional social learning* and *critical social learning*, with environmental stability having a relatively weak influence. The switch typically happens when the cost of asocial learning is around an order of magnitude higher than the cost of social learning. In circumstances in which social learning is effective, then *critical social learning* will be at an advantage, because it will tend to pay the cost of asocial learning less than *conditional social learning*. Conversely, if social learning is ineffective, the reverse is true. Since increased environmental spatial variation decreases the effectiveness of social learning, it will broadly favour *conditional social learning* (see Figure 2.6 and Equation 2.7).

When learning and dispersal are *global* but the environment varies in space, it is very difficult to obtain an appropriate behaviour through social learning. However, *conditional social learning* can invade when asocial learning is relatively unreliable, the environment is highly stable, and, counter-intuitively (since prior theory has found that social learning is favoured when the cost of asocial learning is high, e.g. Boyd and Richerson 1985), when the cost of asocial learning is low. Under these conditions, *conditional social learners* will have an advantage over asocial learners when asocial learning fails, and when there is a chance of learning something useful by social learning, which is higher when the environment is stable. However, the payoff advantage is small, and so will only have an effect when overall learning costs are low, hence the counter-intuitive result of a social learning strategy invading a population of asocial learners when the cost of asocial learning is low. This is also the region where *conditional social learners* outperform *critical social learners*. The latter cannot become established in stable environments because it is difficult for the benefits of social learning to outweigh the low costs of asocial learning.

In some cases pure random social learning could out-compete either of the conditional genotypes for example, when asocial learning was relatively unreliable, N_s was low and c_a was high (Figure 2.5c). This was because a low number of possible environmental states means that even sub-optimal payoffs from pure social learning can be better than more optimal payoffs associated with high learning costs. Here the high probability of acquiring high fitness behaviour means the additional burden of sometimes or always paying the cost of asocial learning carried by the conditional strategies renders them unprofitable. This finding suggests that random copying may be a good strategy in contexts where it is difficult to produce something effective alone, but there is a range of viable alternatives available to copy, all of which may produce something reasonably effective. Aesthetic craft production, such as pottery decoration or rug weaving, may fit these conditions, where the chances of producing something pleasing to the eye oneself may be relatively low, but there are a range of examples available to copy, all of which have previously been selected because they are to some degree, if not equally, pleasing to the eye. Recent evidence reveals that for such traits, neutral drift models provide a good fit. For example, Bentley *et al.* (2004) describe some specific examples of such cultural traits that appear to fit models of random drift that would be expected from random copying. These analyses suggest that these contexts may favour adopting a random copying strategy.

Increasing environmental harshness (*h*) favours the *critical social learning* strategy, and reduced harshness the *conditional social learning* strategy (Figure 2.5d; Equation 2.7). The formulation of Enquist *et al.* (2007), in which only one in an infinite number of behaviour patterns confers any fitness benefit, represents an extreme in the possible distribution of *h* which favours the *critical social learning* strategy. The effect of harshness occurs because both conditional strategies deploy a combination of asocial and social learning, but when *critical social learners* learn asocially, and fail to produce the correct solution, they are allotted a random behaviour. In contrast, when *conditional social learners* learn asocially, and fail to produce the correct solution, they receive the expected payoff of a social learner. Since offspring acquire their parent's behaviour, selection ensures that social learning is likely to acquire behaviour closer, on average, to optimal than random. By magnifying the expected returns to a social learner performing a sub-optimal behaviour (increasing α in Equation 2.7), reduced harshness benefits *conditional social learners*, since *critical social learners* switch to asocial learning if social learning returns sub-optimal behaviour, and therefore risk acquiring a random behaviour rather than satisficing with 'near misses' from social learning.

In summary, using a simple spatially explicit stochastic model, this analysis has shown that spatial structure, including local learning and dispersal, can affect the evolution of social learning in ways that would be difficult to explore and predict using an analytical approach. The simulation framework presented here is potentially a useful vehicle for exploring more complex social learning strategies, such as 'copy-in-proportion', or 'copy-if-better' (Schlag 1998; Laland 2004), which would also be difficult to specify analytically.

SECTION 1, CHAPTER 3

THE EVOLUTION OF TEACHING

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INTRODUCTION

The demographic and ecological success of humanity is widely attributed to our capacity for the high-fidelity information transmission necessary for cumulative culture (Boyd and Richerson 1985; Tomasello 1994). Alongside imitation, teaching is the primary mechanism through which humans pass acquired knowledge, skills and technology between individuals and between generations. Teaching is widespread in human societies, and is a key human psychological adaptation, vital for normative forms of human cooperation to be tenable (Boyd and Richerson 1985; Tomasello 1994; Fehr and Fischbacher 2003; Csibra 2007; Csibra and Gergely 2006), and central to technological development (Boyd and Richerson 1985). Yet if teaching is so effective, it remains a mystery why it should be either absent or exceedingly rare in virtually all other animals.

Countless animals acquire skills and information from others (Heyes and Galef 1996; Laland and Galef 2009), however experienced individuals are not generally thought to actively facilitate learning in others (Danchin *et al.* 2004). Caro and Hauser (1992) proposed a functional definition of 'teaching' applicable to animals, in which a tutor is said to teach if it modifies its behaviour in the presence of a pupil, at some cost, thereby promoting the pupil's learning. Refinements of this definition impose additional criteria, such as feedback from pupil to tutor, or restrict teaching to the transfer of skills, concepts and rules (Franks and Richerson 2006; Leadbeater *et al.* 2006; Hoppitt *et al.* 2008). Deploying such definitions, researchers report putative cases of costly information donation (henceforth 'animal teaching') in diverse species, including ants, bees, pied babblers, meerkats, and cats (Franks and Richerson 2006; Leadbeater *et al.* 2006; Thornton and McAuliffe 2006; Raihani and Ridley 2008; Rapaport and Brown 2008 see Hoppitt *et al.* 2008; Rapaport and Brown

2008 for reviews). While cases of animal teaching remain controversial, and their consanguinity with human teaching is contested (Csibra 2007; Leadbeater *et al.* 2006; Premack 2007), these observations nonetheless raise a challenging question: why should the costly donation of information exhibit such a curious taxonomic distribution?

Any functional similarities should not obscure the fact that mechanistically, cases of animal teaching are entirely different from human teaching, and are not reliant on homologous characters (Csibra and Gergely 2006; Hoppitt *et al.* 2008). Indeed, current thinking suggests that instances of animal teaching function to enhance the fidelity of information transmission through adaptive refinements of forms of learning present in the animal, leading to distinct teaching mechanisms in different species (Hoppitt *et al.* 2008). Nonetheless, it is germane to ask why convergent selection should favour investment in costly mechanisms of information transfer in some species and not others. The fact that functionally similar behaviour is reported in diverse animals, leads us to ask: 'What do these species have in common that led to the evolution of teaching?'; 'Why is teaching not more widespread in animals?;' and 'Why is it that intelligent animals such as chimpanzees seemingly do not teach if ants and bees are capable of doing so?' As animal teaching appears restricted to isolated traits, this raises the further question of: 'How did a very general capability for teaching evolve in the human lineage?'

These questions are of widespread interest to multiple academic disciplines, including Evolutionary and Behavioural Biology, Psychology, Anthropology, Archaeology, Economics and Education. Yet while there has been extensive research into related topics such as the evolution of social learning (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Feldman and Zhivotovsky 1992), learned communication (Boyd, Gintis and Bowles 2010; Kirby, Cornish and Smith 2008; Kirby, Dowman and Griffiths 2007), and learned cooperation (Boyd and Richerson 1985; Fehr and Fischbacher 2003; Gintis 2003; Boyd *et al.* 2003, Peck and Feldman, 1986), currently there is no formal theory of the evolution of teaching.

Here simple and accessible mathematical models are presented, exploring under what circumstances teaching might be expected to evolve. This analysis helps to explain the observed distribution of teaching behaviour, the absence of teaching in other taxa, and the widespread use of teaching in humans.

THE MODEL

First a simple model with haploid genetics is presented but this is later extended to diploid and haplodiploid cases, which give qualitatively similar results. The model assumes a single, infinite-sized, well-mixed population with two genotypes, *teacher* and *non-teacher*. This assumption corresponds to adopting the phenotypic gambit (Grafen, 1984), and in reality it is likely that teaching behaviour will result from an interaction between many genes and experiential factors. Individual fitness is a function of baseline fitness (w_0), costs associated with genotype (c_t, c_c), and a viability benefit (w_i, where $w_i>1$) associated with possessing valuable learned information i. Teaching is costly, with c_c representing a fixed cognitive cost paid by teachers (e.g. representing the neural hardware necessary to teach) and c_t representing a time (or energy) cost paid when teaching. As the cognitive cost of teaching is a cost paid by all teachers independent of their individual fitness, the most appropriate formulation is one in which this cost c_c is additive. Conversely, the time cost, c_t, is dependent on possession of the information, so it is more realistic to view this as multiplicative.

Thus, teachers with and without the information have fitness $w_t=w_0w_ic_t-c_c$ and $w_t=w_0-c_c$, respectively.

Individuals can acquire the information asocially, with probability A, for instance, through trial-and-error learning. However each individual also has a cultural role model, or tutor, from whom they can learn the information, and to whom they are related with relatedness r. Consistent with Grafen's statistical definition (Grafen, 1985, Hamilton, 1970), relatedness is treated as a 'measure of the genetical similarity between social partners, relative to the rest of the population' (West *et al.* 2010). From this role model the individual can acquire the information through inadvertent social learning (e.g. imitation, emulation, enhancement effects), with probability S, or teaching (provided their cultural role model is a teacher), with probability T, where $T>S$ and $T>A$. Pupil and cultural role model combinations form with a probability proportional to their genetic similarity (r). This assumption is consistent with any one of three biologically plausible processes: (*i*) *active choice by pupils*, who adopt cultural role models with a likelihood that increases with relatedness, (*ii*) *active choice by cultural role models*, who adopt pupils with a likelihood that increases with relatedness, or (*iii*) *spatial structure or population viscosity*, leading to related individuals being more likely to assort, and thereby generating pupil/cultural role model pairings, with high compared to low relatedness. Thus while this assortment could result from kin discrimination or a greenbeard mechanism (West *et al.* 2007), it need not do so. A further assumption that each genotype assorts with relatives to a similar degree is also made. This is assumed largely for mathematical convenience and, while it is a defensible first approximation, it may not be met in some natural populations. However, it is possible that there are likely to be greater fitness benefits for assortment amongst teachers than non-teachers, the assumption is likely to translate into conservative estimates of the likelihood of the evolution of teaching. In the terminology of Gardner and West (2006), this treatment of relatedness is more akin to the ‘open’ models of social evolution developed by Frank (1998), than to the explicit ‘closed’ models derived by Taylor (1992) which incorporate levels of dispersal and other demographic assumptions that impact on assortment according to kinship. The frequency of teachers and non-teachers are designated to be t and nt (t+nt=1), the proportion of teachers and non-teachers possessing the information to be i_t and i_{nt}, and the proportion of teachers and non-teachers that do not possess the information to be ni_t and ni_{nt} (i_{nt}+ni_{nt}=1, i_t+ni_t=1), respectively.

First, expressions for the probability that teachers and non-teachers acquire the fitness-enhancing information are developed. As pupil/cultural role model pairings form non-randomly, a focal individual with the teaching genotype shares its genotype through common descent with its cultural role model with probability kr, where k is a scaling constant, thereby acquiring the information through teaching with probability i_tT. Alternatively, with probability 1-kr, the role model’s genotype is not a related teacher and is randomly drawn from the rest of the (infinite) population, giving probabilities that it is an unrelated teacher and non-teacher of t and 1-t, respectively. If the cultural role model is a teacher the focal individual learns through teaching with probability i_tT, whilst if it is not a teacher the probability that the focal individual acquires the information from the role model is $i_{nt}S$. Note that a pupil’s ability to learn from a cultural role model depends critically on the probability that their role model has acquired the information themselves, (i_t and i_{nt} for teachers and non-teachers respectively). This means that individuals may fail to acquire the information with a certain probability regardless of the genotype of their role model. In addition, the focal individual may learn asocially with probability A no matter the genotype of its cultural role model. It follows that an individual with the teaching genotype acquires the information with probability

$$P\left(l \mid t\right) = rki_t T + (1-rk)(ti_t T + (1-t)i_{nt} S) + A\,, \tag{3.1a}$$

and, by similar reasoning, a non-teacher acquires the information with probability

$$P\left(l \mid nt\right) = rki_{nt} S + (1-rk)(ti_t T + (1-t)i_{nt} S) + A\,. \tag{3.1b}$$

The average fitness of teachers and non-teachers is now given by

$$W_t = P(l \mid t)(w_0 w_i c_t) + (1 - P(l \mid t))(w_0) - c_c\,, \tag{3.2a}$$

$$W_{nt} = P(l \mid nt)(w_0 w_i) + (1 - P(l \mid nt))(w_0)\,. \tag{3.2b}$$

The fitness difference between teachers and non-teachers can then be defined as $W_d = W_t - W_{nt}$, such that $W_d > 0$ is the condition for the proportion of teachers to increase in the population. Using expressions (3.1) and (3.2), the model can be specified as a dynamic haploid system in terms of three recursive equations, representing the generational change in frequency of teachers (3.3a), the proportion of teachers with the information (3.3b), and the proportion of non-teachers with the information (3.3c), in the population:

$$t' = \frac{tW_t}{tW_t + (1-t)W_{nt}}\,, \tag{3.3a}$$

$$i_t' = \frac{P(l\,|\,t)(w_0 w_i c_t - c_c)}{P(l\,|\,t)(w_0 w_i c_t - c_c) + (1 - P(l\,|\,t))(w_0 - c_c)}, \tag{3.3b}$$

$$i_{nt}' = \frac{P(l\,|\,nt)(w_0 w_i)}{P(l\,|\,nt)(w_0 w_i) + (1 - P(l\,|\,nt))(w_0)}. \tag{3.3c}$$

Invasion analysis

It is then possible to consider the invasion of teachers into a population of non-teachers. This requires computing the equilibrium frequency of the information amongst non-teachers. Setting $t = 0$ and $k = 1$, simplifying Equation (3.1b), and inserting into Equation (3.3c), generates a simplified recursion in i_{nt}, which can be solved to give

$$i_{nt} = \frac{1 - A - Sw_i + Aw_i \pm \sqrt{Q}}{2S(1 - w_i)}, \tag{3.4}$$

where $Q=4Aw_iS(w_i-1)+(1-A-Sw_i+Aw_i)^2$.

The invasion of teachers at this equilibrium is then explored, assuming that the proportion of teachers with the information is roughly equal to the proportion of non-teachers with the information when teachers are very rare (i.e. $i_t = i_{nt}$). Again $W_d>0$ is the condition for teaching to invade. Thus, in more detail, the condition for the invasion of teaching is

$$w_0(Aw_i(c_t - 1) + i_{nt}Sw_i(c_t - 1) - ri_{nt}(S - T)(c_t w_i - 1)) - c_c > 0. \tag{3.5}$$

For all following analyses the baseline fitness is set to $w_0=1$.

To investigate the dynamics of the system after invasion by a teaching genotype the equation

$$\bar{t} = \frac{\bar{t}W_t}{\bar{t}W_t + (1-\bar{t})W_{nt}} \qquad (3.6)$$

is solved for $\bar{t}$, the equilibrium value of the proportion of teachers in a population. Inspecting equation 3.6, it is clear that the only two biologically possible solutions are $\bar{t}=1$ or $\bar{t}=0$. This means that teachers will either fail to invade or, once they have invaded, will invade to fixation.

Diploid and haplodiploid models

While a model of teaching using haploid genetics is mathematically convenient, the fact remains that teaching animals are perhaps exclusively diploid or haplodiploid in their reproductive systems. The haploid model can be usefully extended to take account of these differences. The model can be reformulated, for example, as a diploid system in which each allele is a teaching allele, *t*, or a non-teaching allele, *nt*. This is achieved by first assuming a heterozygous individual is a teacher with probability *a* and a non-teacher with probability 1- *a*. It is then possible to examine the criteria for teachers invading a population of non-teachers, assuming a negligible number of homozygous teachers (with genotype *tt*) are present, and that all teaching is done by heterozygotes. The probability that a heterozygote (with genotype *tnt*) expresses the teaching gene, and thereby pays the extra time cost (c_t) associated with teaching, is *a*. It follows that the probability that an individual's cultural role model expresses a teaching gene is *ra*. Incorporating this into equation (3.2a) gives

$$W_t = (\alpha r Ti_{nt} + (1-\alpha r)Si_{nt} + A)(w_i(1-\alpha+\alpha c_t)-1)+1-\alpha c_c\,, \qquad (3.7)$$

for a rare teaching mutant in a population of non-teachers. The fitness of the common genotype is the same as in the haploid case, since the probability of a non-teacher encountering a teacher is negligible. Note that when the teaching allele is completely dominant (α=1), equation (3.7) reduces to the haploid expression for W_t (equation 3.2a) with t=0.

To investigate teaching in social insects with haplodiploid reproductive systems, the population is divided into equal male (haploid) and female (diploid) sections. Although a proper treatment of the haplodiploid case may require more direct accounting for the reproductive value of the individuals benefiting from teaching and others who do not, this approximation is a good starting point. In this case, it is assumed that males do not learn the information because the workers (who can use the information) are female. The males, however, may still incur the inherent cognitive cost associated with teaching (c_c) if they carry the teaching allele. They incur this cost despite there being no value to males having the information i.e. $w_i = 1$ for the male section of the population. However these males do not teach and so pay no time cost i.e. c_t=1.

The effects of the individual parameters, discussed above in relation to the haploid model are the same for the diploid model. This similarity occurs because moving from the diploid to the haploid model is a linear transformation and all results from the haploid model hold for the diploid model. These results also hold for a haplodiploid system, where analysis of the invasion criteria for teaching requires consideration of both haploid and diploid offspring. Here it is assumed that the contribution of each sex to fitness is equal, in which case the fitness difference between teachers and non-teachers is

$$w_d = \frac{(w_{t,dip} + w_{t,hap} - w_{nt,dip} - w_{nt,hap})}{2} . \qquad (3.8)$$

Assuming males neither teach nor benefit from teaching (w_i=1 and c_t=1), this reduces to

$$w_{d,hap} = \frac{w_{d,dip} - c_c}{2} . \qquad (3.9)$$

Which reproductive system favours teaching?

From the above, teaching is more likely to invade a haplodiploid than diploid populations if $w_{d,haplodip} > w_{d,dip}$. Assuming that w_i is the same for each reproductive system, this inequality can be written as

$$\frac{w_{d,hap} + w_{d,dip}}{2} > w_{d,dip} \qquad (3.10a)$$

which in turn simplifies to

$$w_{d,hap} > w_{d,dip} . \qquad (3.10b)$$

This means that it is easier for teaching to invade a population of haplodiploid than diploid non-teachers in the same circumstances as it is easier for teaching to invade haploid than diploid non-teachers. Accordingly, using equation (3.2a) for haploids and (3.2b) and (3.7) for diploids,

$$w_{d,dip} = Si_{nt}w_i + (1 - Si_{nt}) - \alpha r_D i_t (S - T)(w_i(1 - \alpha + \alpha c_{tD}) - 1) - \alpha c_{cD} , \qquad (3.11a)$$

$$w_{d,hap} = Si_{nt}w_i + (1 - Si_{nt}) - r_H i_t (S - T)(w_i c_{tH} - 1) - c_{cH} . \qquad (3.11b)$$

Inserting these into inequality (3.10b), re-labelling the relatedness parameters r_H for haploids and r_D for diploids and the costs c_{tD} and c_{tH}, and simplifying, gives the condition under which it is easier for teaching to invade in haplodiploid (and haploid) than in diploid populations

$$\alpha r_D i_t(S-T)(w_i(1-\alpha+\alpha c_{tD})-1)+\alpha c_{cD} > r_H i_t(S-T)(w_i c_{tH}-1)+c_{cH}\,, \qquad (3.12)$$

which if $c_{cD} = c_{cH} = 0$ simplifies to

$$\alpha r_D(1-\alpha+\alpha c_{tD}-\frac{1}{w_i}) < r_H(c_{tH}-\frac{1}{w_i})\,. \qquad (3.13)$$

From this it is clear that where teaching is most likely to evolve depends critically on the dominance of the teaching allele α and the average relatedness of tutor and pupil in diploids and haplodiploids. If w_i is equivalent in the two systems, with complete dominance (α =1) teaching will be more likely in haplodiploids than diploids when $r_H > r_D$, provided that the costs c_{tD} and c_{tH} are comparable.

RESULTS

The relatedness of tutor and pupil

By inspection of Equation 3.5 it is found that teaching will evolve where its costs are outweighed by the inclusive fitness benefits that result from the tutor's relatives being more likely to acquire the valuable information. This effect echoes both recent and traditional formulations of inclusive fitness models first proposed by Hamilton

(1964). The impact of relatedness in this model follows more closely the inclusive fitness formulation described by Hamilton (1964) and examined by Taylor *et al.* (2007), concentrating on the fitness effects of an individual's behaviour on kin and the population as a whole. The benefit to possessing the teacher genotype comes from an increased chance that the individual's cultural role model will also be a teacher, which leads to a greater probability of acquiring the information. As might be expected, the benefits of teaching are sensitive to the relatedness of tutor and pupil. Any fitness advantage to teaching depends critically on teachers having a higher than average probability of learning from their cultural role model. The change in fitness associated with r when teachers invade is $-ri_{nt}(T-S)(w_i c_t - 1)$ and when non-teachers invade is $-ri_t(T-S)(w_i - 1)$. The more related an average individual is to its role model the greater the benefit of teaching (Figure 3.1a), a finding consistent with both existing kin selection theory and recent verbal arguments concerning the evolution of teaching (Hoppitt *et al.* 2008; Thornton and Raihani 2008).

The effects of asocial and inadvertent social learning

The effects of asocial and inadvertent social learning (A and S) on equation 3.5 are similar and can be dealt with together. Of particular significance is the finding of *n*-shaped functions representing how the utility of teaching is affected by other means of acquiring the information (Figure 3.1b). Effective asocial or social learning, represented by high values of A or S relative to T, reduces the benefits of teaching, rendering it uneconomical. As asocial learning and inadvertent social learning are less costly than teaching, non-teachers have a fitness advantage over teachers when the information is easy to acquire. These observations explain why the incidence of teaching does not appear to co-vary with brain size or intelligence in animals.

Teaching will not be favoured where the pupil can easily acquire the information on its own, or through copying others (Hoppitt *et al.* 2008; Thornton and Raihani 2008). This is apparent in primates such as chimpanzees, which are very efficient learners and are thought to be particularly adept at social learning and imitation (Whiten *et al.* 2003; Whiten 2005). Paradoxically, the models in this chapter also establish that teaching is not generally favoured for difficult to learn traits (low A and S), as teachers typically do not possess the information to pass on to their relatives. Accordingly, teaching is most likely to be favoured by mid-range A and S values, with the breadth of the window within which teaching invades dependent on the fitness benefits of the information (w_i). However, unless w_i is very high, there will typically be an extremely narrow range of traits for which teaching would be efficacious, which helps to explain both the rarity of teaching in nature and the highly specific nature of animal teaching. For example, meerkat helpers teach pups to process scorpions and other food items, but not what to eat, nor any non-foraging behaviour (Thornton and McAuliffe 2006). Similarly ants, social bees and babblers also teach a single highly specific piece of information (Franks and Richardson 2006; Leadbeater *et al.* 2006; Hoppitt *et al.* 2008; Raihani and Ridley 2008).

When considering the invasion of teachers into a population of non-teachers A and S have two conflicting effects. Firstly, increasing both A and S relative to T reduces the value of teaching by increasing the probability of learning by other means. Since asocial learning and inadvertent social learning are less costly than teaching, non-teachers have a fitness advantage over teachers when the information is easy to acquire. Intuitively, as the gap between S and T closes the benefits to teaching diminish. High values of A and S, corresponding to cases where the information is easy to acquire through other means (i.e. without teaching), thus do not favour teaching.

Secondly, the indirect effect of increasing *A* and *S* is to increase the amount of information in the population, which increases the benefit of being a teacher over that of being a non-teacher (*see below)*. Conversely, very low values of *A* and *S* do not favour teaching, since teachers typically do not possess the information to pass on to their relatives. Teaching is most likely to be favoured by mid-range *A* and *S* values, while very easy and very difficult to learn traits do not promote teaching (see Figure 3.1b). The effect of asocial learning (*A*) also depends on the relative values of social learning (*S)* and teaching efficacy (*T)*. As the gap between *S* and *T* closes, an increase in *A* favours non-teachers. In other words, under these circumstances the advantage for a teacher diminishes. This occurs because non-teachers can pass the information on at no cost. One ramification of these observations is that there is little incentive for otherwise effective learners to teach. This is discussed by Whiten (1999) in relation to the great apes who are extremely effective learners but appear to display little or no teaching behaviour.

The value of information

Any benefit to being a teacher comes from an increased chance that the individual's cultural role model will also be a teacher, which leads to a greater probability of acquiring the information. It follows that this benefit increases with the proportion of individuals in the population possessing the information. To be explicit $P(l \mid t) - P(l \mid nt) = r(Ti_t - Si_{nt})$, thus if both i_t and i_{nt} are increased by ε, the difference in probability of learning as a teacher and as a non-teacher, $P(l|t)$ - $P(l|nt)$, is increased by $\varepsilon r(T - S)$, which is positive. However, as the information in the population increases, the fitness of both genotypes increases because, since $T > S$, teachers bring more information into the population than non-teachers. This leads to the counter-intuitive result that the fitness of non-teachers W_{nt} can increase when the cost of teaching is decreased.

Cumulative culture model

Compared to animal teaching, human teaching is a very general capability, reliant on high-fidelity mechanisms such as speech, instruction, and direct shaping, and it allows the transmission of complex information that could not be devised by a single individual (Hoppitt *et al.* 2008). Humans have undergone cumulative cultural evolution, which has in essence reduced our reliance on information acquired asocially, and allowed the transfer of knowledge and skills that would be difficult to learn without direct guidance and instruction. Valuable information concerning, for instance, industrial practices or technological manufacture has become available to teach through the accumulated efforts of many individuals.

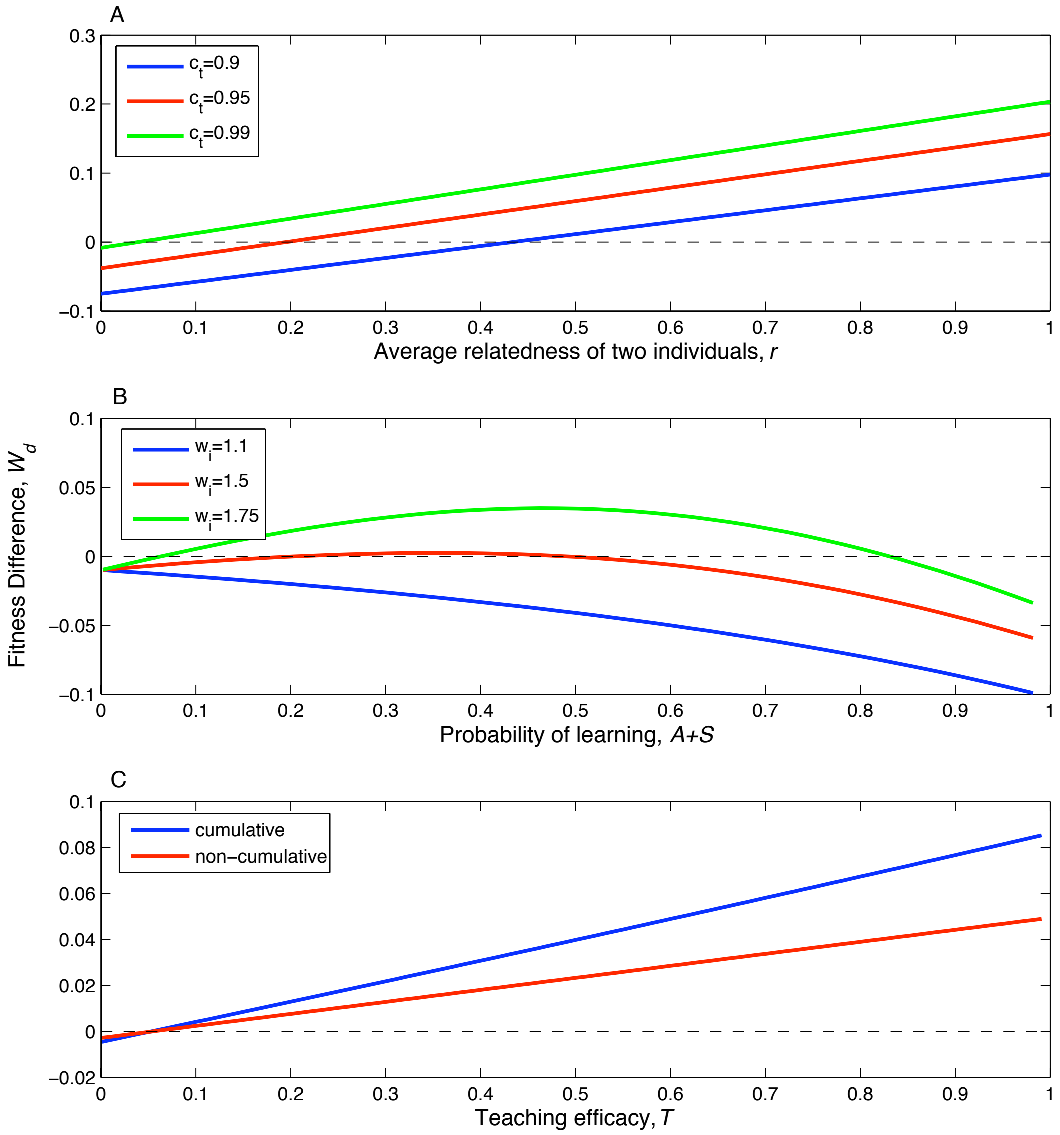

Figure 3.1. (*A*) Fitness difference between teachers and non-teachers (w_d), plotted against the average degree of relatedness between an individual and its cultural role model, for different values of c_t. Above the dashed horizontal line teachers are more fit than non-teachers and can invade. T=0.9, c_c=0.001, w_i=2, S=0.5, A=0.1, w_0=1. (*B*) w_d plotted against the probability of learning through means other than teaching, for three values of w_i. T=0.9, r=0.5, c_t=0.915, c_c=0.01, w_0=1. (*C*) w_d plotted against teaching efficacy, T, for a cumulative and a non-cumulative model. A_1=A_2=S_1=S_2=0.05, c_c=0.0001, w_1=2, w_2=6, r=0.5, w_0=1, c_t=0.99. Note the difference in scale of effects on the y-axes of the three plots.

It is possible, using this model, to explore whether teaching and cumulative culture might have coevolved, extending the simple model presented above to allow for cumulative knowledge gain by allowing individuals that have acquired the information to gather further knowledge, building on and improving the information, simultaneously making it more fitness enhancing but more difficult to learn. The model assumes two pieces of information (*1* and *2*), the latter refining the former, where individuals with both pieces of information gain fitness increment $w_1 w_2$ with $w_2 > 1$. The evolution of teaching in humans can be investigated by exploring how cumulative learning affects the sensitivity of the invasion conditions to the fidelity of teaching, *T*, and the value of the information w_i. Including a second round of learning where the pupils who learnt in the first round get a chance to learn the second trait from a new cultural parent captures the essence of cumulative knowledge gain. It is then possible to rebuild the model using equations 3.1a and 3.1b.

An expression describing the likelihood that any teacher will teach twice is generated, this is the likelihood that their new pupil has already acquired information *1* and so is capable of learning information *2,* given that they themselves have both pieces of information available to teach. An expression for this is given by the sum of the probability that the teacher's second student is a teacher itself, multiplied by the probability that a teacher picked up information *1*, and the probability that the student is a non-teacher multiplied by the probability that a non-teacher could have picked up information *1*:

$$L_T = (r + (1-r)t)P(l_1 \mid t) + (1-r)(1-t)P(l_1 \mid nt)\,. \tag{3.7}$$

Using this it is possible to calculate the equilibrium frequency of information *2* in the population when teachers are very rare:

$$\hat{i}_{nt_2} = \frac{P(l_1 \mid nt)P(l_2 \mid nt)(w_0 w_1 w_2)}{P(l_1 \mid nt)P(l_2 \mid nt)(w_0 w_1 w_2) + P(l_1 \mid nt)(1 - P(l_2 \mid nt))(w_0 w_1) + (1 - P(l_1 \mid nt))w_0}\,. \tag{3.8}$$

The fitness functions for teachers and non-teachers are the calculated for individuals in a population where teaching is rare, these are:

$$\begin{aligned} W_t &= (P(l_1 \mid t) - P(l_1 \mid t)P(l_2 \mid t))(w_0 w_1 c_t) + (P(l_1 \mid t)P(l_2 \mid t)) \\ &\quad (w_0 w_1 w_2 c_t (1 - L_T + ct(L_T))) + (1 - P(l_1 \mid t))(w_0) - c_c \end{aligned} \tag{3.9a}$$

$$\begin{aligned} W_{nt} &= (P(l_1 \mid nt) - P(l_1 \mid nt)P(l_2 \mid nt))(w_0 w_1) + \\ &\quad (P(l_1 \mid nt)P(l_2 \mid nt))(w_0 w_1 w_2) + (1 - P(l_1 \mid nt))(w_0) \end{aligned} \tag{3.9b}$$

Using these it is possible to analyse the difference in fitness between teachers and non-teachers in a population of mostly non-teachers in three different conditions: a cumulative culture where the second trait is a refinement of the first (i.e. $1 < w_2$); a non-cumulative culture ($1 = w_2$); and the original model with no second trait. The presence of a second trait that does not refine the first is similar to having two independent traits that give the same fitness benefit which can be picked up in sequence.

Numerical analysis of these three conditions shows that the fitness advantage of teachers over non-teachers is greater in a cumulative culture context than a non-cumulative context, and that this fitness difference increases with the fidelity of teaching (as T increases) (see figure 3.1c). Writing W_{dc} for the fitness difference between teachers and non-teachers in the cumulative setting, and retaining W_d for the non-cumulative setting, figure 3.2 shows that W_{dc} - W_d is positive across most biologically plausible conditions. This means that the relative fitness of the teaching compared to the non-teaching genotype is always the same or higher in a cumulative setting compared to a non-cumulative setting, and this conclusion holds across an extremely wide range of parameter values. Furthermore, numerical analysis has established that, for biologically plausible values of the relevant parameters (T, A, S, w_i, c_t), the equilibrium frequency of information in the population prior to the invasion of teaching is always higher in a cumulative setting than in a non-cumulative one (see Figure 3.2d). Naturally, additional cumulative learning episodes would further increase W_{dc} - W_d. Conversely, a second learning opportunity when $w_1 \geq w_1 w_2$ does not increase a teacher's fitness. Thus the difference between the cumulative and non-cumulative model is *not* explained by the fact that there are two learning opportunities in the cumulative setting.

Figure 3.1c illustrates how cumulative knowledge gain increases the difference in fitness between teachers and non-teachers, broadening the range of conditions under which teaching evolves, and figure 3.2 reveals that this pattern is robust across all biologically plausible parameter space. The fitness advantage of teaching over non-teaching increases with the fidelity of teaching (T), and does so more sharply in a cumulative compared with a non-cumulative setting.

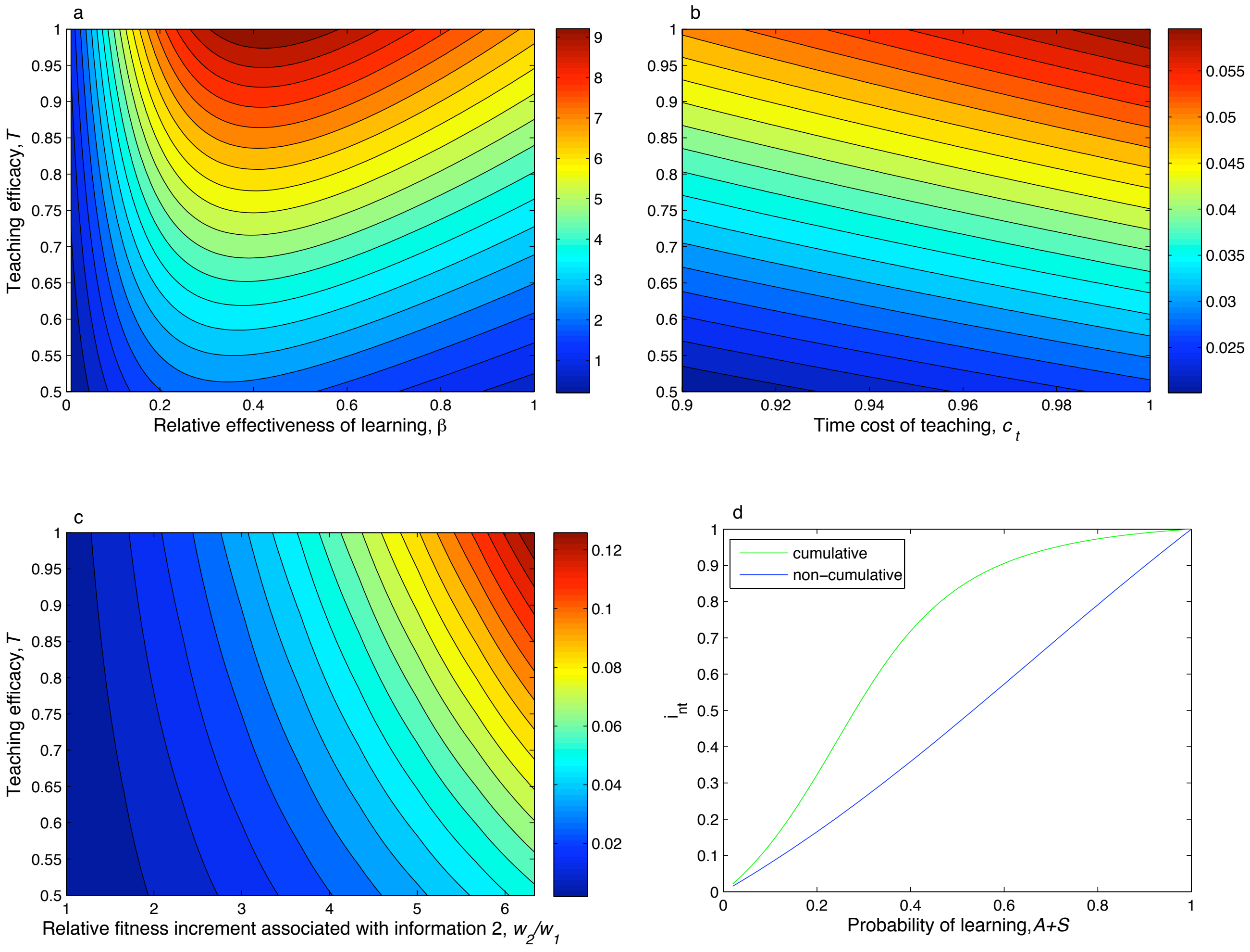

Figure 3.2. The fitness advantage of teaching over non-teaching is greater in a cumulative compared to a non-cumulative setting (i.e. W_{dc} - $W_d > 0$), across a broad range of parameter space. Contour plots show W_{dc} - W_d, with teaching efficacy, T ($0.5<T<1$) plotted against (*a*) the relative ease of learning information 2 compared to information 1 (henceforth b, where $A_1=bA_2$ and $S_1=bS_2$. As b approaches 1, information 2 becomes as easy to learn as information 1, through asocial and inadvertent social learning), (*b*) the time cost of teaching, c_t, and (*c*) the fitness value of information 2, w_2. (*d*) The equilibrium frequency of information *1* is higher in a cumulative than a non-cumulative setting. In all plots $A_1=A_2=S_1=S_2=0.05$, $c_c=0.0001$, $w_1=1.5$, $w_2=6$, $r=1/2$, $w_0=1$, $c_t=0.99$ except where otherwise stated.

Data collection for model testing.

It may be possible for researchers to collect data with which to parameterise and test the predictions of the models described above. The generation of values for the efficacy of asocial and inadvertent social learning (*A* and *S*) parameters is relatively straightforward and useful values have already been generated by Thornton and McAuliffe (2006) regarding meerkats (although not in sufficiently high numbers to allow their use here). Patterns of relatedness (*r*) for tutors and pupils could feasibly be extracted from patterns of social interaction, using Grafen's (1985) statistical approach. In order to generate a relative likelihood of the invasion of teaching between two species, a reasonable approximation would be to assume that the parameters describing the absolute worth of the information (w_i) and the baseline fitness value (w_0) were equal across species. Since in most cases it is possible to set the cognitive cost of teaching to be zero ($c_c = 0$), the only remaining parameters relate to the value of the time cost to each individual teacher, c_t. In cases where teaching has been observed, for example in meerkats, this data may readily be estimated. In cases where teaching has not been previously seen, different values of c_t within a sensible range could be used to compare the likelihood of teaching under different circumstances. Accordingly, the above analyses provide opportunities for the emergence of a theory driven empirical science of animal teaching.

DISCUSSION

The evolution of teaching has been explored here using simple mathematical models in which a single tutor transmits adaptive information to a related pupil at a cost. Teaching is expected to evolve where its costs are outweighed by the inclusive fitness benefits that result from the tutor's relatives being more likely to acquire the valuable information. The models show that teaching is not favoured where the pupil can easily acquire the information on its own or through copying others, nor for difficult to learn traits where teachers typically do not possess the information to pass on to their relatives. This leads to a narrow range of traits for which teaching would be efficacious which helps to explain the rarity of teaching in nature, its unusual distribution, and its highly specific nature. Further models that allow for cumulative cultural knowledge gain suggest that teaching evolved in humans despite, rather than because of, our strong imitative capabilities, and primarily because cumulative culture renders otherwise difficult-to-acquire valuable information available to teach.

Although the extent of animal teaching may, as yet, have been underestimated (Hoppitt *et al.* 2008; Thornton and Raihani 2008; Laland and Hoppitt 2003), nonetheless the generality and pervasiveness of human teaching offers a striking contrast to teaching in other animals. This analysis suggests that this follows from two factors unique to our species. First, by virtue of our capacity for language, pedagogical cueing, teaching through imitation, manual shaping, and mental state attribution (which allows tutors to adjust their teaching to the state of knowledge of the pupil) (Premack 2007; Tomasello and Call 1997), the fidelity of human teaching (T) is likely to be unusually high relative to teaching in other animals (Tomasello 1994; Csibra 2007; Csibra and Gergely 2006). Second, cumulative cultural evolution allows complex, high fitness (Boyd and Richerson 1985; Henrich and McElreath 2003) traits that no individual could acquire on his or her own or through inadvertent social learning ranging from ancestral lithic technology, tools, and weaponry through to contemporary technology, to be present and available to teach in human populations.

The analysis here implies that teaching and cumulative culture reinforce each other, and may have coevolved, because teaching is more advantageous in a cumulative culture setting, whilst cumulative knowledge gain is frequently reliant on teaching. This may be why teaching is observed in humans but is rare or absent in old world primates (Rapaport and Brown 2008), which by most accounts do not possess cumulative culture (Tomasello 1994). In populations that lack cumulative culture, difficult to acquire information would not reach sufficiently high frequency to promote teaching. While there are reports that teaching is not common in some hunter-gatherer societies (e.g. Whiten *et al.* 2003), such reports refer to an absence of direct instruction and neglect the prevalence of more subtle forms of teaching, such as pedagogical cueing (Csibra and Gergely 2006).

A small subset of animals do appear to satisfy the stringent conditions for teaching to evolve, and the findings presented here may also shed light on the taxonomic distribution of teaching. For instance, the possibility of higher relatedness amongst female workers in the social insects than amongst diploid relatives may help to explain why teaching is observed in some tandem running ants and some social bees (Franks and Richardson 2006; Leadbeater *et al.* 2006; Hoppitt *et al.* 2008; Thornton and McAuliffe 2006), but rarely in vertebrates (although strong conclusions over the frequency of teaching are difficult in the absence of experimental confirmation of teaching in a number of cases (e.g. cats) where circumstantial evidence for teaching exists). Formal analyses of diploid and haplodiploid systems presented in this chapter establish the precise conditions under which teaching will evolve in these genetic systems. This suggests that there are likely to be circumstances in which teaching evolves more readily among haplodiploid workers than in diploids, other factors being equal, because of the possibility of higher levels of relatedness between workers in relatively monogamous haplodiploid colonies (Cornwallis *et al.* 2010; see Craig 1979 and Foster *et al.* 2006 for discussion of relatedness in haplodiploids).

It also seems to be the case that the most compelling cases of animal teaching occur in cooperatively breeding species (ants, bees, meerkats, pied babblers) - indeed humans too have been characterised as cooperative breeders (Hrdy 1999). Relative to non-cooperative breeders, cooperative-breeding helpers engage in costly (Thornton and McAuliffe 2006), and prolonged (Langen 2000), provisioning of the young, providing a selective environment for adaptations that would speed up the transition to independent feeding. It is possible that in cooperative breeders, the alleviation of heavy provisioning costs, or sharing of costs amongst multiple tutors, corresponds to a significantly lower *per capita* cost (c_t) to an individual teacher, which Figure 3.1a shows helps render teaching economical. Teaching may be favoured only where the tutor's operational costs are low (Thornton and Raihani 2008). Moreover, cooperative breeders often exhibit high levels of relatedness (Cornwallis *et al.* 2010), further enhancing the likelihood of teaching evolving. The obvious counter-examples are felids, where teaching of young by mothers may perhaps be favoured because hunting skills, or the opportunities to gain them, are difficult to get through asocial or inadvertent social learning (corresponding to low A and S but high T in this model).

In cases where teaching does evolve, the average fitness of all individuals in the population increases, implying that teaching may have group beneficial properties. This analysis could usefully be extended to multiple competing populations where growth in populations capable of teaching, with group augmentation which favours cooperative breeding (Kokko *et al.* 2001), potentially further promoting teaching could be seen. The models presented here could usefully be extended to include direct benefits, and it is plausible that if such direct benefits are high and the costs are low, the likelihood of teaching amongst non-relatives may increase.

Cooperation is defined as behaviour that provides a benefit to another individual (recipient), and that is selected for because of its beneficial effect on the recipient (West *et al.* 2007). Whilst in humans it is possible for an individual to be taught non-beneficial traits (e.g. to take Class A drugs, or become a suicide bomber), the overwhelming majority of cases of teaching in humans, and all known cases of teaching in other animals, meet this definition of cooperation. One might ask, if most instances of teaching are also acts of cooperation, given the extensive literature on the evolution of cooperation (Sachs *et al.* 2004; Lehmann & Keller 2006; West *et al.* 2007), is a specialized treatment of the evolution of teaching necessary? This question must be answered in the affirmative because teaching is a special case of cooperation, with unique properties that need to be incorporated into formal models in order to generate accurate predictions.

One property of teaching is that an individual's fitness depends not only on whether or not they possess the teaching genotype, but also whether or not they possess the acquired information or skill. In this respect, teachers resemble the 'phenotypic defectors' incorporated into some cooperation models (Lotem *et al.* 1999; Sherratt & Roberts, 2001), who are unable to cooperate through lack of physical resources (i.e. if sick or young). Central to the teaching model is the assumption that individuals can acquire information through means other than being taught (for instance, through individual learning or inadvertent social learning). For example, individuals can be taught to capture scorpions, to fashion a hand-axe or to solve differential equations, but with varying probabilities they can also acquire this knowledge on their own through trial-and-error learning, or through imitation and other forms of copying. This would be analogous to individuals receiving the fitness benefits of cooperation without cooperation taking place. However, at least in principle, individuals could acquire physical resources either through their own efforts (analogous to asocial learning), through scrounging (analogous to inadvertent social learning), or as recipients of cooperative acts (analogous to being taught). An important consequence of these alternative means of knowledge gain is that they potentially disconnect the frequency of teachers from the frequency of individuals with the relevant information or skill. Moreover, the frequency of this information amongst individuals possessing the teaching genotype is, in part, a function of the frequency of the information in the population at large (see equation 3.1a). Accordingly, in order to predict when a teaching event will occur (which is essential to investigate its evolution), it is necessary additionally to track the frequency of the information in the sub-populations, and not just allele, genotype, or phenotype frequencies. It is difficult to find any model of cooperation that, in addition to the donation of physical resources by cooperators, also allows physical resources to be acquired both through individual's own efforts and through scrounging, and moreover that also tracks resource frequencies as dynamic variables amongst co-operators and non-cooperators. Furthermore, were such a model to be formulated it would still exhibit different dynamics to the teaching model presented here. That is because physical resources and informational resources have quite different dynamical properties. For instance, an informed individual can exploit the information without depleting it, and can pass it on to others without hindering their ability to utilise it themselves. In addition, the fitness of the teaching genotype increases the more information there is in the population, since the teachers need to know the information to pass it on to their relatives. At the same time, the amount of information increases with the number of teachers (since teachers are better at spreading information than non-teachers). This is in contrast to most models of cooperation, where the benefit to defection tends to grow as cooperation becomes more common.

In these respects the treatment of teaching also differs from previous models of the cultural evolution of cooperative behaviour (e.g. Henrich & Boyd 2001; Boyd *et al.* 2003; Bowles and Gintis 2004), which have not distinguished between asocial learning, inadvertent social learning and teaching. As a result of this lack of distinction, the frequency of cooperative behaviour is directly related to the frequency of socially transmitted information. Recent theory suggests that asocial learning could plausibly play an important role in cooperative behaviour and needs to be incorporated into cultural evolution models (Lehmann *et al.* 2008). The findings of the teaching analysis support this argument. The most interesting results of this model, that teaching is not favoured both for very difficult and very easy to learn traits (figure 3.1b), and is promoted by cumulative culture (figures 3.1c, 3.2), stem directly from this disconnect between the frequency of the teaching genotype and the frequency of the information to be taught, and the idiosyncratic properties of information flow.

These differences mean that the problem of the evolution of teaching does not reduce to the problem of the evolution of cooperation in any general form, at least not in a straightforward manner such that established theory fully explains the evolution of teaching. While some of the more intuitive findings from the teaching model (e.g. that the likelihood of teaching increases with the degree of relatedness between tutor and pupil and decreases with the costs of teaching, figure 3.1a) are unsurprising in the light of current understanding of evolution of cooperation (Sachs *et al.* 2004; West *et al.* 2007), the more significant and novel findings emerge solely from this treatment.

Recent thinking within anthropology supports the argument that teaching is widespread in humans (Tehrani and Riede 2008; Hewlett *et al.* 2011), in spite of earlier claims to the contrary (e.g. McDonald 2007; Lewis 2007), but that teaching takes on a variety of forms from direct verbal instruction to more subtle pedagogical cueing. The models presented in this chapter imply that teaching may be widespread in humans because cumulative cultural knowledge-gain renders otherwise difficult to learn, high-fitness information available for tutors to impart. While it is frequently claimed that human cooperation is unique (Boyd and Richerson 1988a; Henrich 2004), it is not immediately clear in what respects (West *et al.* 2010). This analysis provides one possible answer to this conundrum. West *et al.* (2010) point out that 'complex and unique mechanisms to enforce cooperation have arisen in humans, such as contracts, laws, justice, trade and social norms…' It is likely that all of these mechanisms require teaching to spread. Human cooperation may, therefore, be unusually extensive as a result of cumulative culture and may be uniquely reliant on an important mechanism less frequently observed in other species: teaching.

SECTION 2:

THE SOCIAL LEARNING STRATEGIES TOURNAMENT

SECTION 2, CHAPTER 4

WHY COPY OTHERS? INSIGHTS FROM THE SOCIAL LEARNING STRATEGIES TOURNAMENT

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INTRODUCTION

Human culture is widely thought to underlie the extraordinary demographic success of our species, manifest in virtually every terrestrial habitat (Richerson and Boyd 2005, Cavalli-Sforza and Feldman 1981). Cultural processes facilitate the spread of adaptive knowledge, accumulated over generations, allowing individuals to acquire vital life skills. One of the foundations of culture is social learning – learning influenced by observation or interaction with other individuals (Heyes 1994) – which occurs widely, in various forms, across the animal kingdom (Hoppitt and Laland 2008). Yet it remains something of a mystery why it pays individuals to copy others, and how best to do this.

At first sight, social learning appears advantageous because it allows individuals to avoid the costs, in terms of effort and risk, of trial-and-error learning. However, social learning can also cost time and effort, and theoretical work reveals that it can be error prone, leading individuals to acquire inappropriate or outdated information in non-uniform and changing environments (Boyd and Richerson 1985, Rogers 1988, Feldman *et al.* 1996, Kameda and Nakanishi 2003, Giraldeau *et al.* 2003, Wakano *et al.* 2004, Enquist *et al.* 2007). Current theory suggests that to avoid these errors individuals should be selective in when and how they use social learning, so as to balance its advantages against the risks inherent in its indiscriminate use (Giraldeau *et al.* 2003). Accordingly, natural selection is expected to have favoured social learning strategies, psychological mechanisms that specify when individuals copy, and from whom they learn (Laland 2004, Kendal *et al.* 2009).

These issues lie at the interface of multiple academic fields, spanning the sciences, social sciences and humanities, from artificial intelligence to zoology (Boyd and Richerson 1985, Danchin *et al.* 2004, Apesteguia *et al.* 2007, Whitehead *et al.*

2004, Dautenhahn and Nehaniv 2002, Schlag 1998). Formal theoretical analyses (e.g. Cavalli-sforza and Feldman 1981, Boyd and Richerson 1985, Rogers 1988, Feldman *et al.* 1996, Kameda and Nakanishi 2003, Giraldeau *et al.* 2003, Enquist *et al.* 2007, Laland 2004, Kendal *et al.* 2009, Henrich and McElreath 2003) and experimental studies (Kendal *et al.* 2009, Galef 2009) have explored a small number of plausible learning strategies. While insightful, this work has focussed on simple rules that can be studied with analytical methods, and can only explore a tiny subset of strategies. For a more authoritative understanding of when to acquire information from others, and how best to do so, the relative merits of a large number of alternative social learning strategies must be assessed. To address this, here a large-scale computer tournament in which strategies competed in a complex and changing simulation environment is presented. €10,000 was offered as first prize to the winner of the tournament. The organisation of similar tournaments by Robert Axelrod in the 1980s proved an extremely effective means for investigating the evolution of cooperation, and is widely credited with invigorating that field (Axelrod and Hamilton1981).

THE TOURNAMENT

Tournament structure

The simulation environment was represented as a 'restless multi-armed bandit' encompassing 100 possible behavioural acts (represented arbitrarily by the integer's 1-100) and a payoff associated with each act. Axelrod's cooperation tournaments were based on a widely accepted theoretical framework for the study of cooperation – the Prisoner's Dilemma. While there is no such currently established framework for social learning research, multi-armed bandits have been widely deployed to study learning across biology, economics, artificial intelligence research and computer science (e.g. Schlag 1998, Koulouriotis and Xanthopoulos 2008, Gross *et al.* 2008, Bergman and Valimaki 1996, Niño-Mora 2007, Auer *et al.* 2002) because they mimic a common problem faced by individuals that must make decisions about how to allocate their time in order to maximize their payoffs. Multi-armed bandits capture the essence of many difficult problems in the real world, for instance, where there are many possible actions, only a few of which yield a high payoff, where it is possible to learn asocially or through observation of others, where copying error occurs and where the environment changes. When the payoffs of a multi-armed bandit change over time, as in the tournament, the bandit is termed 'restless', and the framework has the advantage of proving extremely difficult, perhaps impossible, to optimize analytically (e.g. Papadimitriou and Tsitsiklis 1999). Thus it was possible to be confident that the tournament would be a genuine challenge for all entrants.

In all other respects the model structure was kept as simple as possible to maintain breadth of applicability and ease of understanding, and attract the maximum number of participants. This simplicity was balanced with the inclusion of three critical features, namely, individual memories (to facilitate learning), a degree of error associated with social learning (the existence of which nearly all the current literature agrees on), and replicator dynamics with mutation, to allow an evolutionary process. Time was used as a common currency for costs and each possible move cost the same, to minimise structural assumptions. The agents in each simulation could not identify or communicate directly with each other, an assumption that precluded the deployment of some model-based strategies present in the cultural evolution literature (e.g. prestige bias Henrich and Gil-White 2001). Nonetheless, it was reasoned that the simplicity, accessibility and generality of the proposed tournament structure outweighed the benefits of further complexity.

As mentioned above, the simulation environment contained 100 possible acts. The payoff for each available act was an integer drawn at random from an exponential distribution (λ=1; values were squared, then doubled, and finally rounded to give integers mostly falling in the range 0-50). Payoffs changed between rounds with independent probability p_c, with new payoffs drawn at random from the same distribution. This information was kept deliberately vague to participants, so as to discourage overly specific solutions.

Each simulation contained a population of 100 agents each possessing a behavioural repertoire, which was empty at the start of the agent's life. An agent's repertoire could subsequently only gain acts through some form of learning. To gain behaviours or payoffs, entered strategies had to specify how individual agents, in a finite population, choose between three possible moves in each round, namely INNOVATE, OBSERVE and EXPLOIT. INNOVATE represented asocial learning, or individual learning through direct interaction with the environment, for example through trial-and-error. An INNOVATE move always returned accurate information about the payoff of a randomly selected behaviour previously unknown to the agent. OBSERVE represented any form of social learning or copying through which an agent could acquire a behaviour performed by another individual, whether by observation of or interaction with that individual (Heyes 1994). An OBSERVE move returned information about the behaviour and payoff currently being demonstrated in the population by one or more other agents playing EXPLOIT. OBSERVE was error prone with regard to both act and payoff. OBSERVE returned a different act to that performed by the observed agent with probability $p_{copyActWrong}$, with the learned act selected at random from the 99 not being performed, although the payoff learned was still that of the observed agent. Independently, the returned payoff estimate was subject to normally distributed random error (rounded to the nearest integer) with mean 0 and standard deviation $\sigma_{payoffError}$ (with the returned payoff estimate lower bounded at 0). Playing OBSERVE could return no behaviour if none were demonstrated, or if a behaviour that was already in the agent's repertoire was observed. The probabilities of these errors occurring, and the number of agents observed, were varied parameters. Finally, EXPLOIT represented the performance of a behaviour from the agent's repertoire, equivalent to pulling one of the multi-armed bandit's levers. An individual could only EXPLOIT behavioural acts it had previously learned. When an individual chose to EXPLOIT an act, it received the current payoff specified in the environment. Note that this value could differ from the expected payoff held in the agent's behavioural repertoire, for two reasons. Firstly, the payoff for an act could have changed in the rounds since it was learned or last exploited (with probability p_c each round). Secondly, if the act was learned in an OBSERVE move, then the payoff could have been subject to error. When an agent played EXPLOIT, it could, by performing an act, update its knowledge of how profitable that act was, and store the updated information in its behavioural repertoire. These moves are summarised in Table 4.1.

The role of the entered strategies was to specify which of these three moves an agent should play in each simulation round, with optional reference to information that was made available to that agent (the agent's history and behavioural repertoire) Each agent was controlled by one of the entered strategies, assigned at the start of its life and agents did not change strategy during their lives.

Table 4.1: Move available to agents in the tournament simulation

Move (represents)	**Information gained**	**Payoff**
INNOVATE (Asocial learning)	Act and payoff (without error) randomly chosen from those currently unknown to the agent.	None.
OBSERVE (Social learning)	Act and payoff of $n_{observe}$ demonstrators chosen at random from those playing EXPLOIT in the previous round. $N(0, \sigma_{payoffError})$ error always added to payoff information. Incorrect, randomly chosen, act returned with probability $p_{copyActWrong}$.	None.
EXPLOIT (Performing behaviour)	Current actual payoff of chosen act.	Current payoff of chosen act.

Agents could remember their own history of moves and payoffs, as well as their current behavioural repertoire. Along with the number of rounds the agent had been alive, this history and behavioural repertoire was the only information available to the entered strategies when deciding which move an agent should play. Evolutionary change was modelled as a death-birth process. Within a simulation, agents died with probability 0.02 per round, giving an expected lifespan of 50 rounds. Dying individuals were replaced by the offspring of agents selected to reproduce from those surviving with probability proportional to the agent's mean lifetime payoff P defined as the sum of all its payoffs from playing EXPLOIT during its life, divided by the number of rounds it had been alive. The probability of individual z reproducing was $P_z / \Sigma P$, where ΣP was the summed mean lifetime payoff of the population in that round.

Offspring usually carried their parent's strategy, except for a small probability of mutation, in which case the offspring carried one of the other strategies available in the simulation. While the mutation rate used (0.02) was quite high relative to natural rates of mutation in eukaryotes, reducing this rate did not qualitatively affect the outcomes, and the higher rate offers significant computational advantages in terms of time to equilibrium.

The tournament received 104 entries, most, though not all, from academics across a wide range of disciplines, and from all over the world. The tournament was run in two stages. Strategies first competed in pairwise round-robin contests, taking turns to invade, or to resist invasion by, another strategy under a single set of conditions (strategy performance was unaffected by whether they were the invading or invaded strategy - Pearson correlation between invading and invaded scores, $r = 0.9998$, $p < 0.0001$). The ten best performers progressed to a second stage, where all ten strategies competed simultaneously in melee contests over a range of simulation conditions. Scores in the first stage ranged from 0.02 to 0.89 (with a theoretical maximum of 1), indicating considerable variation in strategy effectiveness (shown in Figure 4.4a).

Strategy evaluation Stage I: Round-robin pair-wise contests

Strategies first took part in pair-wise contests against all other strategies. Each pair-wise contest consisted of 10 simulations in which agents performing strategy A were introduced (using the mutation process described above) into a population containing only strategy B, and the reciprocal 10 simulations in which B was introduced into A-dominated populations. This reciprocal invasion approach was used to ensure that the findings were robust to strategies' initial frequencies. In each simulation, a population of the dominant strategy was introduced and run for 100 rounds without mutation so that agents could establish their behavioural repertoires. Mutation was then introduced, providing the second strategy the opportunity to invade, and simulations were run for a further 10,000 rounds. The mean frequency of a strategy over the last 2,500 simulation rounds was its score for that simulation. Simulation scores were then averaged over the 20 simulations, and this average recorded as the contest score for that strategy in that contest. Strategies were ranked on their average contest score once they had played against every other strategy. These simulations were run with the parameter set [p_c=0.01, $n_{observe}$=1, $p_{copyActWrong}$=0.05, $\sigma_{payoffError}$=1]. This stage involved 5,356 paired contests, with 107,120 (5,356×20) individual simulation runs.

Initially, it was planned that the 10 highest scoring strategies would carry through to the next tournament phase, however the division cut off a series of strategies (ranked 6 to 24) with relatively small differences in their scores such that the initial ranking could plausibly have been dependent on the set of conditions (Figure 4.4a inset). Since it was important to be confident that the success of the 10 best strategies was not due a chance match of any strategy to the specific single parameter set, more pair-wise contests on the top 24 strategies were run across a range of conditions.

It was computationally feasible to run a further 8 conditions for the subset of strategies ranking in the top 24 of the first set of contests; these conditions are set out in Table 4.2. Note that the parameter $\sigma_{copyPayoffError}$ was not varied in these conditions, as the parameter $p_{copyActWrong}$ affected the accuracy of social learning in a similar manner but to a stronger degree; to vary $\sigma_{copyPayoffError}$ orthogonally would unnecessarily duplicate effort in exploring the effect of the accuracy of social learning as well as doubling the computation time required. A single pair-wise simulation with two extra conditions was run, varying $\sigma_{copyPayoffError}$ from the initial condition above [p_c=0.01, $n_{observe}$=1, $p_{copyActWrong}$=0.05, $\sigma_{copyPayoffError}$=5], and [p_c=0.01, $n_{observe}$=1, $p_{copyActWrong}$=0.05, $\sigma_{copyPayoffError}$=10]. For all of these further conditions the number of repetitions per contest was reduced to 3 symmetric repetitions (i.e. 3 runs with strategy A as invader and 3 runs with strategy B as invader) as opposed to the 10 such repetitions run for the initial pair-wise contest. The value 3 was selected based on Figure 4.1, which shows that the distribution of coefficient of variation values for each pair-wise contest does not change for more than 3 repetitions.

Table 4.2: Details of further conditions run for top 24 strategies

Condition	p_c	$n_{observe}$	$p_{copyActWrong}$	$\sigma_{copyPayoffError}$
1	0.001	1	0.01	1
2	0.1	1	0.01	1
3	0.001	1	0.1	1
4	0.1	1	0.1	1
5	0.001	6	0.01	1
6	0.1	6	0.01	1
7	0.001	6	0.1	1
8	0.1	6	0.1	1

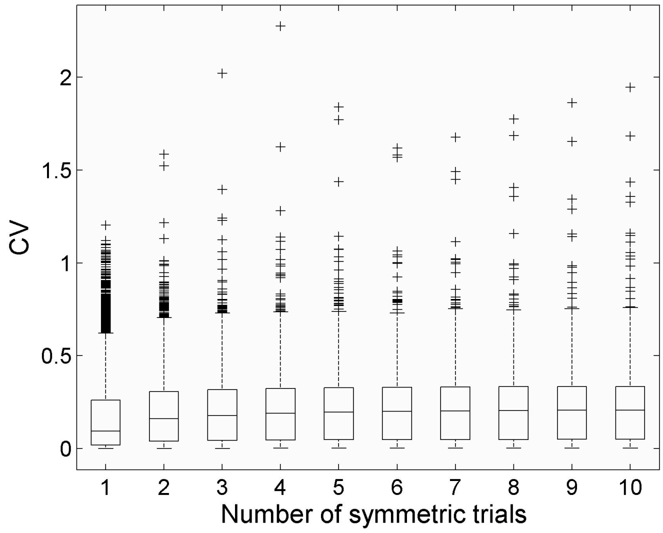

Figure 4.1: Boxplot of pair-wise coefficient of variation distributions by number of repetitions.

These additional analyses required 13,248 further simulation runs (23×24×3×8). No strategy switched from the original pair-wise results by more than 11 places, and the average change in rank was 2.5 places, suggesting it was highly unlikely that any strategies outside the top 24 would have been elevated into the top 10. The extra conditions resulted in two strategies from the original best 10 (*senescence* and *observe3ThenExploit*) being dropped in favour of two others (*livingdog* and *valueVariance*) that had initially ranked 13 and 15 respectively.

Strategy evaluation Stage II: Melee contests

In the melee stage simulations, all ten of the strategies selected in Stage I competed simultaneously. Each simulation started with a population consisting of a simple strategy that did not use any social learning, but played INNOVATE on the first round of its life and subsequently played EXPLOIT continually with the single act that it acquired on the first round (this strategy was entered independently in the tournament as *exploitOneInnovation*. It did not progress past the pairwise phase, ranking 102nd). This strategy was used to avoid giving any of the ten competing strategies any advantage or disadvantage from being established in the population before the invasion of the others. Mutation was introduced from round 1, providing the competing strategies with equal opportunity to invade. Simulations were run for 10,000 rounds, but mutation was turned off in the last quarter (i.e. rounds 7,500 – 10,000). The mean frequencies of each strategy over the last quarter of each run were recorded as the scores for each strategy in that simulation. Strategies were then ranked on their average score across all simulations.

Two sets of conditions were run, termed *systematic* and *random*. For the systematic condition set, a number of values for each of the four parameters were selected, p_c, $n_{observe}$, $p_{copyActWrong}$, and $\sigma_{copyPayoffError}$ (Table 4.3). Fifty simulations were run with each of the 280 possible combinations of these parameter values giving 14,000 simulations. To check that the results of this process were not unduly affected by the specific parameter values chosen, random conditions, where parameter values were chosen at random from statistical distributions weighted in accordance with the values chosen for the systematic conditions were also run (Figure 4.2). These distributions were weighted toward lower values of p_c, $n_{observe}$, and $p_{copyActWrong}$ because higher values of these parameters were considered to be less biologically or ecologically plausible than lower ones. 1,000 unique sets of parameter values were selected in this way and a single simulation run with each set of values, giving a further 1,000 simulations. Systematic and random analyses gave identical returns on the ranked performance of the 10 strategies, computed across all simulations and based on their frequency in the last quarter of each simulation. Accordingly strategy scores were averaged over all 15,000 melee simulations to give the final scores.

Table 4.3: Details of further conditions run for top 10 strategies; values in bold are those used for the main pair-wise contest in Stage I.

Parameter	Values
p_c	0.001, 0.005, **0.01**, 0.05, 0.1, 0.2, 0.4
$n_{observe}$	**1**, 2, 6, 12
$p_{copyActWrong}$	0.01, **0.05**, 0.1, 0.25, 0.5
$\sigma_{copyPayoffError}$	**1**, 10

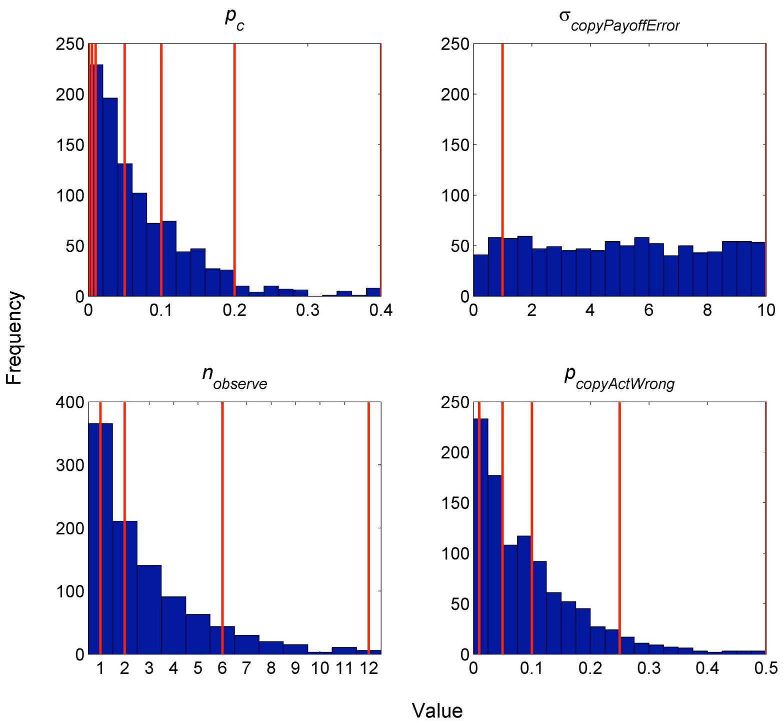

Figure 4.2: Distributions of parameter values chosen for melee (Stage II). Blue bars are histograms of values chosen for the random conditions, red lines show values selected for systematic conditions.

All simulations were run in the Matlab®/Octave computing environment, using both the UK National Grid Service and desktop computers. Entries could take the form of Matlab®/Octave code or prose pseudocode; in the latter case, the pseudocode was converted to real code. Coding errors were guarded against by recoding each strategy using a second independent coder, and testing that each version produced exactly identical results when given the same input sequences, including identical sequences of randomly-generated numbers when strategies made decisions stochastically. Strategies were restricted to take, on average, no longer than 25 times the duration of an example strategy provided in the rules to return a decision. No strategy failed this criterion, and there was no relationship at all between computation time and score in the pair-wise phase of the tournament (Figure 4.3).

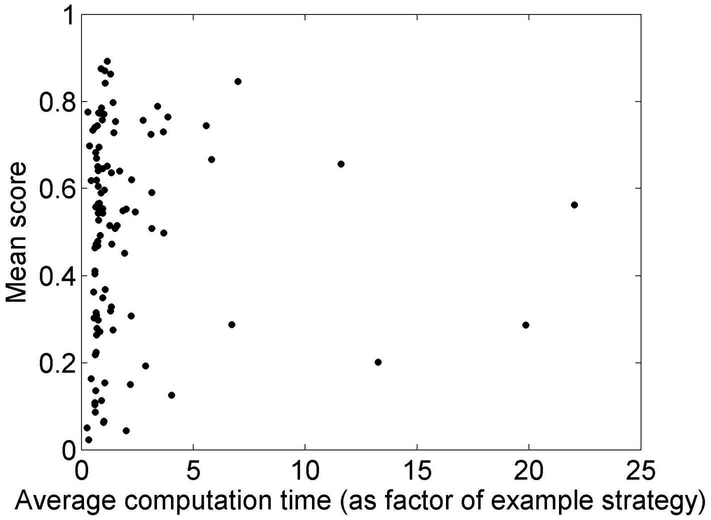

Figure 4.3: Strategy scores in pair-wise tournament phase plotted against the average per-round computation time, expressed as a multiple of the time taken by an example strategy.

Statistical analyses

The factors that made a strategy successful in the pair-wise-contests (Stage I) were examined using linear multiple regression and model selection, with contest score as the dependent variable. For each strategy, a range of possible predictors of a strategy's score was established (Table 4.4), and these were entered into an all-possible-subsets model comparison procedure. The analysis was run with all strategies and subsequently with only the top 24 to see if the same factors were responsible for success in the broadest context and when competing only against successful strategies. In each case, the package 'leaps' in the statistical package *R* was used to return the five best models for each subset of predictors, selected by Mallow's Cp. The model that minimised Akaike's Information Criterion (AIC) was then selected, although results were very similar when model selection was based on Bayesian Information Criterion (BIC). Finally, predictor effect sizes were calculated as beta weights using the package 'yhat'.

Table 4.4: Predictors entered into model selection

Predictor name	Explanation
Check central payoff? (Y=1, N=0)	Categorical variable indicating whether a strategy checked any central tendency (e.g. mean) in the payoff values in the agent's history, either from learning or EXPLOIT.
Check mean EXPLOIT? (Y=1, N=0)	Categorical variable indicating whether a strategy checked the mean payoff from playing EXPLOIT in the agent's history.
Estimate $n_{Observe}$? (Y=1, N=0)	Categorical variable indicating whether a strategy estimated the value of the parameter $n_{Observe}$.
Estimate p_c? (Y=1, N=0)	Categorical variable indicating whether a strategy estimated the rate of environmental change as given by the parameter p_c.
Flexible behavior? (Y=1, N=0)	Categorical variable indicating whether a strategy's choice of move was affected by the outcome of previous moves, or always followed a predetermined series of moves.
Log of variance in rounds to EXPLOIT	Pooled variance, across all agents with the strategy, in the number of rounds between the 'birth' of an agent with the strategy and the first time the agent played EXPLOIT (continuous measure). The log of this value was used as exploratory analysis showed a log-linear relationship with score.
Mean rounds between learning moves	Average number of rounds between any learning moves (OBSERVE or INNOVATE), across all agents with the strategy (continuous).
Proportion of learning moves	Average proportion of moves dedicated to learning (either OBSERVE or INNOVATE), across all agents with the strategy (continuous).
Proportion of learning that is OBSERVE	Average proportion of learning moves that were OBSERVE, across all agents with the strategy (continuous).
Stochastic? (Y=1, N=0)	Categorical variable indicating whether a strategy ever chose between actions stochastically, i.e. dependent on the draw of a random number.

RESULTS

Statistical analysis of all 104 strategies returned a best model containing 5 predictors of a strategy's score, although not all were significant at $\alpha = 0.05$ in that model (Table 4.5). Strong effects of "Proportion of learning that is OBSERVE" and "Variance in time to first EXPLOIT" and moderate effects of "Proportion of learning moves" and "Average rounds between learning moves" were detected. The categorical variable indicating whether a strategy estimated the rate of environmental change apparently had a positive effect, but high variability within categories meant that the mean effects were not significant at $\alpha = 0.05$ (Figure 4.5a). When the same analysis was restricted to just the 24 top-scoring strategies a different, and reduced, set of predictors emerged (Table 4.6). However, the best-fit model in this analysis was not able to explain as much variation as the analysis with all strategies.

In this reduced model, the categorical variable indicating whether a strategy had flexible behaviour was retained with the largest effect size, in place of the variable indicating whether a strategy estimated the value of p_c (Figure 4.5b). The proportion of learning moves was retained with a large negative effect. The log of the variance in time to EXPLOIT was also retained with a significant negative effect, as in the model with all strategies. Two predictors present in the model with all strategies were dropped in this model - the proportion of learning moves dedicated to OBSERVE, and the categorical variable indicating whether a strategy estimated the rate of environmental change. Finally, the mean number of rounds between learning moves had a significant effect in both analyses. However, the effect is in opposite directions when considering data from all strategies, where there is an apparent positive relationship, compared to data from only the top 24 strategies, where the effect is negative (Figure 4.6). Thus, when competing against other effective strategies, it was detrimental to leave too many rounds between learning moves.

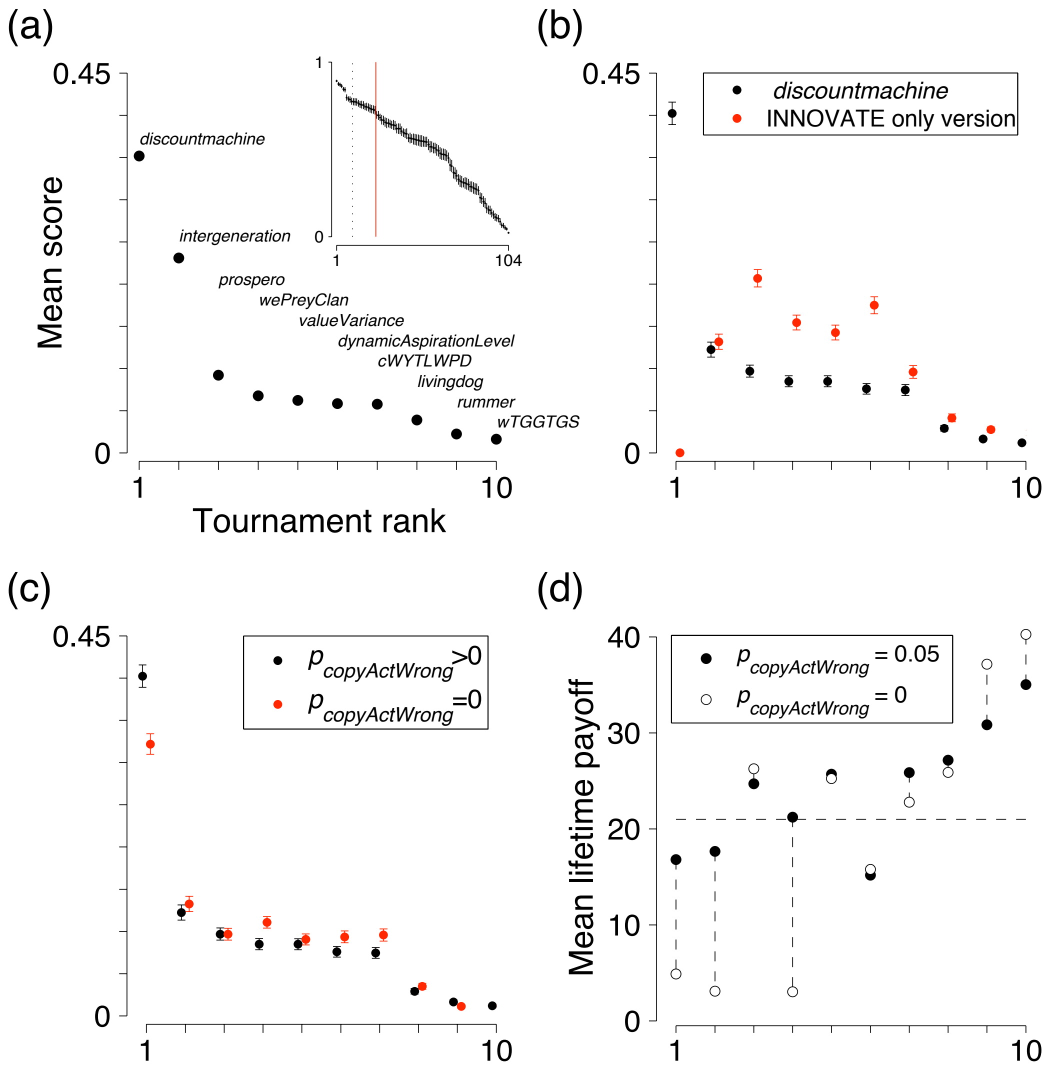

Figure 4.4: Performance of entered strategies. (a) Ranked overall strategy scores in the final stage of the tournament (*cWYTLWPD* = *copyWhenYoungThenLearnWhen-PayoffsDrop* and *wTGGTGS* = *whenTheGoingGetsToughGetScrounging*). Scores are averaged over all final stage simulations. Inset shows scores for all 104 entered strategies. Dotted black line indicates the ten highest scoring strategies; solid red line indicates the 24 strategies entered into further pair-wise conditions. (b) Ranked scores from those final stage simulations in which conditions were chosen at random (*33*), and under the same conditions but with the tournament winner, *discountmachine*, re-coded to learn only with INNOVATE and never OBSERVE (red). (c) As (b) but comparing original results with $p_{copyActWrong}$ fixed at 0 (red). (d) Average individual fitness, measured as mean lifetime payoff, in populations containing only single strategies for each of the final stage contestants, ranked by tournament placing. Data are average values from the last quarter of single simulations, run under the same conditions as the first stage of the tournament, and also under the same conditions except with $p_{copyActWrong} = 0$. The horizontal dashed line represents the mean lifetime payoff of individuals when all strategies are played together under the same conditions. Strategies relying exclusively on social learning are those ranked 1, 2 and 4. Error bars are ± SEM, but mostly not visible as all SEMs<0.004.

Table 4.5: Parameters of the *AIC* best-fit model predicting strategy scores in the first, pairwise, tournament stage. Adjusted R^2=0.76.

Predictor	**Effect size (β weight)**	β	**S.E.**	t	$p(>\|t\|)$
(Intercept)	-	0.32	0.06	5.43	<0.0001
Proportion of learning that is OBSERVE	0.42	0.43	0.06	7.15	<0.0001
Variance in rounds to first EXPLOIT*	-0.42	-0.06	0.01	-6.62	<0.0001
Proportion of learning moves	-0.17	-0.34	0.12	-2.79	0.0063
Average rounds between learning moves	0.16	0.01	<0.01	3.09	0.0026
Estimate p_c? (Y=1, N=0)	-0.07	-0.04	0.03	-1.47	0.1452

* natural log of this predictor was used to give a better linear relationship

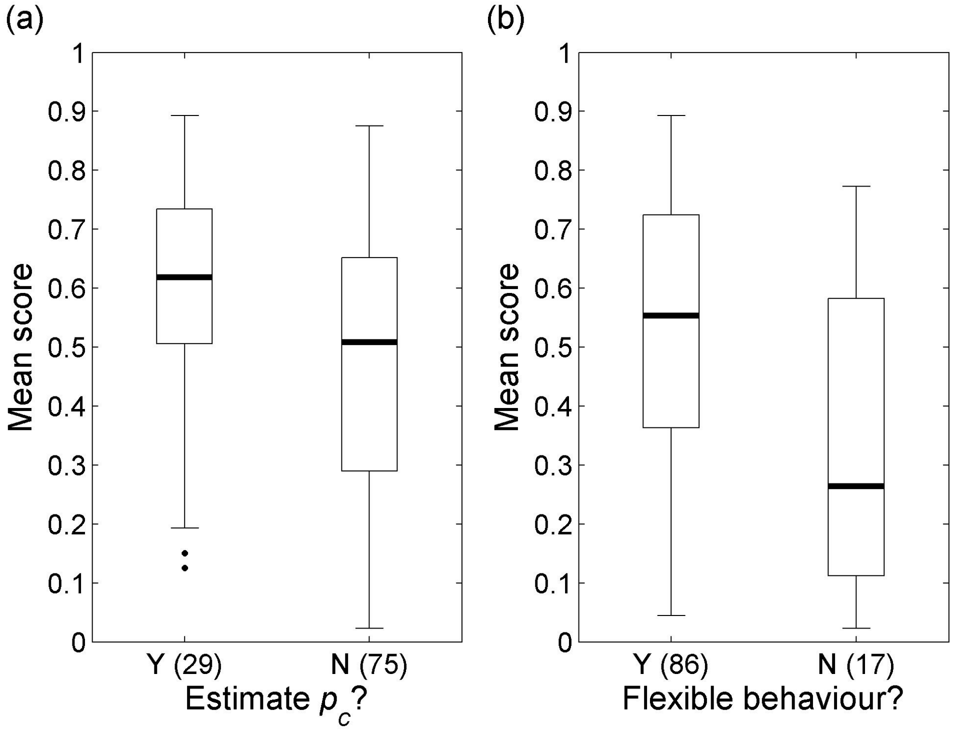

Figure 4.5: Box plots showing scores for strategies that did or did not (*a*) estimate the rate of environmental change and (*b*) have flexible behaviour in the sense that behaviour was conditional on the move history or current repertoire of an agent. Data are from pair-wise contests.

Table 4.6: Best model for pair-wise strategy scores using top 24 strategies only. Adjusted R^2=0.50.

Predictor	**Effect size (β weight)**	**β**	**S.E.**	**t**	**$p(>\|t\|)$**
(Intercept)	-	0.98	0.14	6.95	<0.0001
Flexible behavior? (Y=1, N=0)	0.69	0.34	0.13	2.75	0.0127
Proportion of learning moves	-0.64	-2.74	0.78	-3.52	0.0023
Average rounds between learning moves	-0.61	-0.01	0.01	-2.35	0.0298
Variance in rounds to first EXPLOIT*	-0.47	-0.05	0.02	-3.11	0.0058

*We used the natural log of this predictor to give a better linear relationship

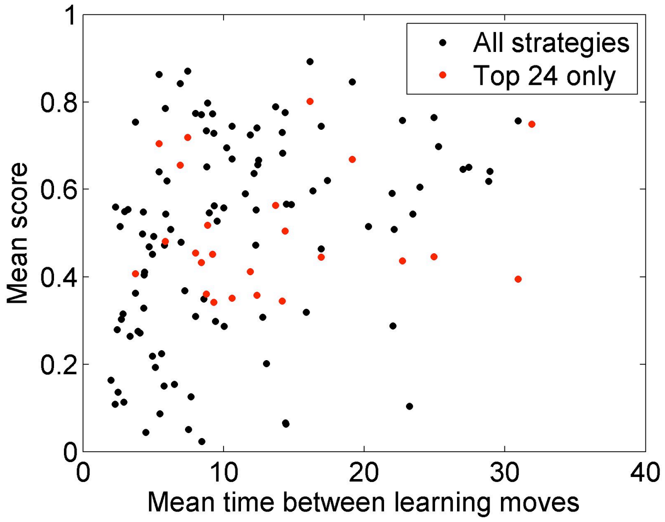

Figure 4.6: Final score against the mean number of rounds between learning moves. Data from all pair-wise contests are labelled ‘All strategies’ data restricted to contests between the top 24 strategies are labelled ‘Top 24 only’. Note that for the latter, the mean score is calculated from contests involving only those 24 strategies, so appear lower than might initially be expected.

The ten highest scoring strategies from the pair-wise phase then progressed to the melee phase, in which all ten strategies competed simultaneously in series of simulations across a broad range of parameter values. Strategies were ranked according to their score averaged over all melee simulations. The highest scoring strategy in this phase, and therefore the tournament winner, *discountmachine*, was the same strategy that scored highest in the first, pair-wise, phase, and scored highest in both the random and systematic analysis of the melee. This strategy won convincingly, although with the second placed strategy, *intergeneration*, it formed a pair of strategies that performed markedly better than the other contenders (Figure 4.4a).

All ten melee strategies were responsive to changes in the rate of environmental variation in that they all increased the amount of learning they did at higher rates of variation (Figure 4.7a). Most strategies continued to increase the amount of learning as variation rates increased, although four did not, including the top two, in that they appeared to cap the amount of learning they did even as rates of environmental change continued to increase. The second placed strategy stands out has having the lowest learning rates of all the melee contenders. While all strategies continued to learn to some extent throughout the agent's lives, the winner stood out by distributing learning almost equally across different phases of life (Figure 4.7b). In contrast, the second placed strategy had the highest variance in learning rates, concentrating over 60% of its learning in the first third of the agent's lives. This contrast goes some way to explaining the relative performance of the strategies in varying rates of environmental change. When the environment is relatively static, low learning rates overall and a concentration at the beginning of life are advantageous to *intergeneration*, as the acquired information is less likely to change, while in changeable environments, the higher lifelong learning rates of *discountmachine* give it the upper hand.

When learning, all melee strategies used OBSERVE at least 50% of the time, regardless of the conditions (Figure 4.7c-d). There was a great deal of variation in how strategies changed their use of social and asocial learning as conditions varied. Notably, the top two ranked strategies, as well as two others (*wePreyClan* and *dynamicAspirationLevel*, ranked 4th and 6th respectively) played OBSERVE almost all the time, regardless of how much the environment was changing (Figure 4.7c) or what the relative costs of social and asocial learning were (Figure 4.7d). The other strategies showed a variety of responses to both variables, with some increasing the amount of social learning with increasing environmental variation and reduced cost of social learning, and others decreasing the amount of social learning under the same conditions.

The timing of (either form of) learning also emerged as a crucial factor. Strategies with a high variance in the number of rounds spent learning before the agent first played EXPLOIT, caused by occasionally waiting too long before beginning to exploit, tended to do poorly (Figure 4.8b). Conversely, strategies that engaged in longer bouts of exploiting between learning moves tended to do significantly better (Figure 4.8d). In general, successful strategies were able to target the timing of their learning moves effectively, increasing the amount of learning in periods immediately following significant drops in average lifetime payoff in the population caused by environmental change that reduced the payoff of a commonly exploited act, but also quickly dropping back to low levels of learning so as to maximize the amount of exploiting (Figure 4.8c). To quantify this, the maximum absolute lagged Pearson correlation value was calculated between the time series of the average lifetime payoff in the population and the proportion of the population playing a learning move, for 200 of the random melee simulations. To compare this with less effective strategies, the strategy *piRounds*, that chose an action based on the digit of π that corresponded to the age of an agent (i.e. behaved at random) and which ranked 88 in the pair-wise phase, and the nine strategies ranked immediately above it were selected, and calculated the same maximum correlation values for these strategies when they played 200 rounds under the same conditions.

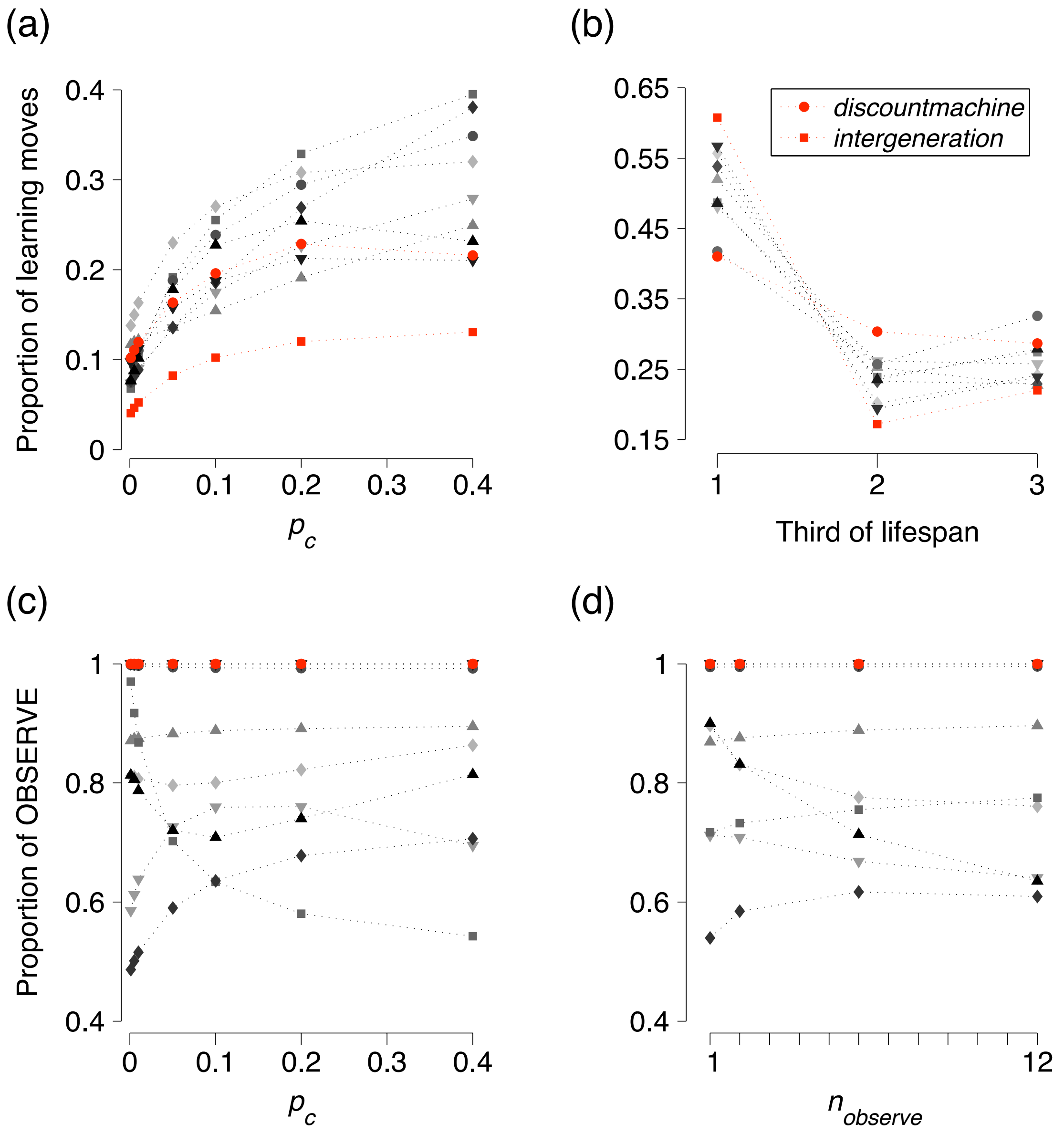

Figure 4.7: Why the winner won. (a) Proportion and (b) timing of learning moves in the final tournament stage. First and second place strategies are highlighted; the rank of the other strategies is indicated by shading, with darker shading indicating higher rank. (c-d) Variation in the proportion of learning moves that were OBSERVE with (c) variation in the rate of environmental change (p_c) and (d) the number of agents sampled when playing OBSERVE ($n_{observe}$), in the final tournament stage. Error bars are ± SEM, but mostly not visible as all SEMs<0.003

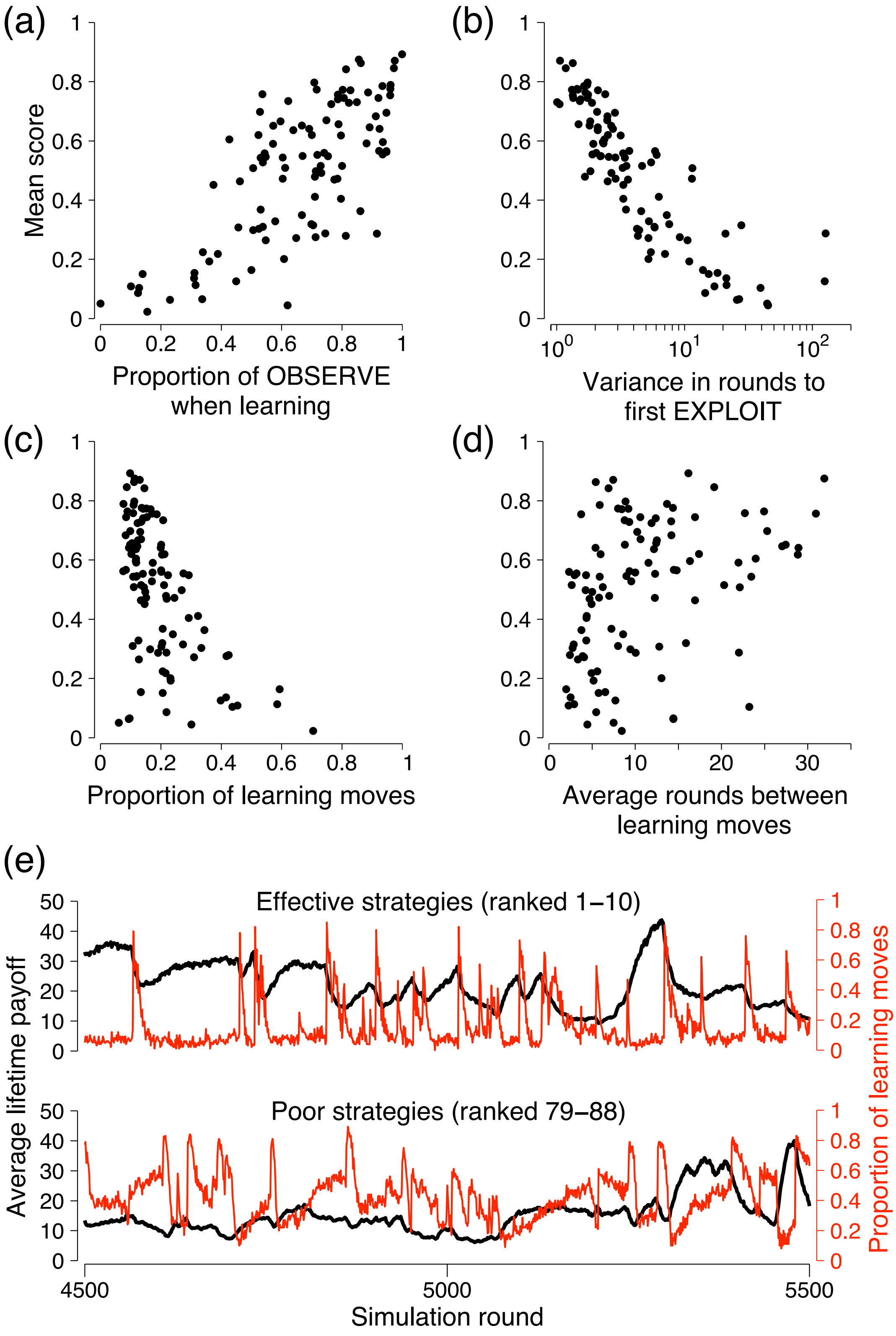

Figure 4.8: Key variables affecting strategy performance. (a) Final score plotted against the proportion of learning (i.e. INNOVATE or OBSERVE) moves that were OBSERVE in the first tournament stage. (b) Final score against the variance in the number of rounds before the first EXPLOIT. (c) Final score against the proportion of rounds spent learning in the first tournament stage. In both, each point represents the average value for one strategy. (d) Final score against the mean number of rounds

between learning moves. (e) Time series plots of the per-round average individual mean lifetime payoff in the population and proportion of learning moves, from 1000 simulation rounds run under identical conditions with the final stage contestants (top panel) and the strategies ranked 79-88 in the first tournament stage (lower panel).

For melee strategies, the largest absolute correlations were always negative (Figure 4.9), and always with a positive lag of 1 or 2, indicating a rapid increase in learning almost immediately after payoff drops. In contrast, the maximum correlations for the less effective strategies were less strong, not always negative and occurred at a more diverse range of lags. Successful strategies targeted learning to periods when it was likely to be most valuable (i.e. when the environment changed) but otherwise minimised learning, allowing them both to improve their payoffs through learning, and to maintain high rates of exploiting. The issue of when to break off exploiting current knowledge in order to invest in further knowledge gain – the exploitation/exploration trade-off – had not been incorporated into previous theory in this field, and the tournament introduces this new dimension into the domain of understanding social learning.

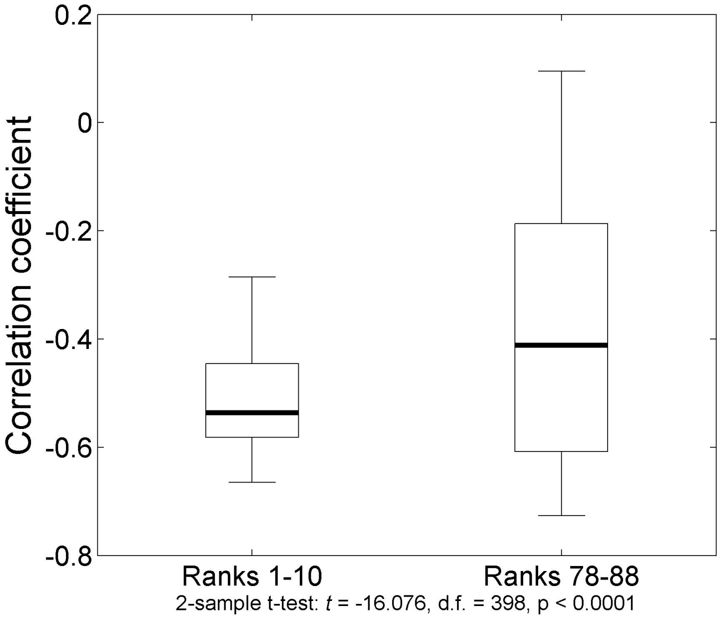

Figure 4.9: Boxplot of maximum absolute lagged Pearson correlation values between average lifetime payoff and proportion of learning in a population for effective (Rank 1-10) and less effective (Rank 78-88) strategies.

The timing of learning was not, however, the only key to success. The winning strategy stood out by spreading learning more evenly across agent lifespans than any other second stage strategy (Figure 4.7b). It did this by using a proxy of geometric discounting to estimate expected future payoffs from either learning or playing EXPLOIT. Importantly, it also relied more heavily on recently acquired than older information. The top two strategies shared the following expression for estimating the expected payoff ($w_{expected}$) of a known behaviour:

$$w_{\mathrm{exp}} = w\left(1 - p_{est}\right)^{i} + \bar{w}_{est}\left(1 - \left(1 - p_{est}\right)^{i}\right), \qquad (4.1)$$

where w is the current payoff held in the agent's memory and acquired i rounds ago, $\bar{w}_{est}$ is the estimated mean payoff for all behaviour, and p_{est} is an estimate of p_c, the probability of payoff change. This expression weights expected payoffs increasingly towards an estimated mean as the time since information was last obtained increases. Given the uncertain and potentially conflicting nature of information obtained through social learning, the winning strategy used a further weighting based on its estimate of p_c, discounting older social information more severely in more variable environments than in relatively constant ones. No other strategies in the melee round evaluated payoffs in this way (See Chapter 6 for a full discussion).

The winning strategy used social learning virtually exclusively – it would play INNOVATE only on the second round of an agent's life if, after playing OBSERVE on the first, there was no behaviour observed, i.e. no other agent in the population played EXPLOIT. That this reliance on social learning was crucial to its success is shown by the results of running the random conditions melee again but with a version of *discountmachine* re-coded to learn only by playing INNOVATE (Figure 4.4b). In this analysis, the innovate-only version places last against the other melee strategies, and, interestingly, other strategies change scores significantly, such that the second placed tournament strategy does not win and is instead overtaken by 4 other strategies. This result suggests that there are frequency-dependent effects present. Seemingly, *discountmachine* inhibits the fitness of other melee strategies when it relies exclusively on OBSERVE.

Previous theory suggests that reliance on social learning should not necessarily raise the average fitness of individuals in a population (Rogers 1988, Feldman *et al.* 1996*,* Wakano *et al.* 2004), and may even depress it (see Chapter 2).This was not the case with the melee strategies in the tournament where average lifetime payoff was positively correlated with proportion of OBSERVE moves (Figure 4.10a). It was also possible to look at this relationship for strategies that had performed relatively poorly in the first, pair-wise, phase of the tournament, running 200 random condition melee rounds with the strategies that ranked 78-88 for comparison. Poorly performing strategies showed a relationship between average individual fitness and the rate of social learning that was strongly negative (Figure 4.10b), the opposite of the result for the melee strategies. This highlights the importance of the strategic use of social learning in raising the average fitness in a population (Boyd and Richerson 1985, Laland 2004, Henrich and McElreath 2003).

This contrast between the results and previous theory can be explained by noting that the tournament structure contained a mechanism by which social learning can result in new behaviour entering the population, through the parameter $p_{copyActWrong}$, the probability that OBSERVE returns not the observed act, but another randomly selected act. When 200 random condition melee rounds were run with the melee strategies with $p_{copyActWrong}$ set to zero, the positive correlation between average individual fitness and the rate of social learning amongst melee strategies disappeared and became instead strongly negative (r = -0.30, p < 0.001; Figure 4.10c). Thus, when there is no copy error, high levels of social learning are associated with reduced average individual fitness in the population.

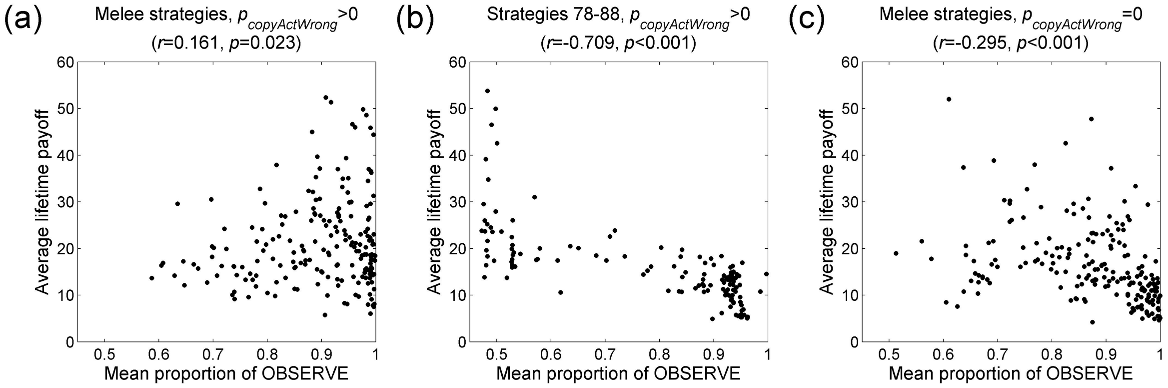

Figure 4.10: The average lifetime payoff in a population against the mean proportion of OBSERVE when learning, for (a) strategies in melee phase with $p_{copyActWrong}$ > 0, (b) strategies ranked 78-88 in pair-wise phase with $p_{copyActWrong}$ > 0, and (c) strategies in melee phase with $p_{copyActWrong}$ fixed at 0. Results are means over the last quarter of 200 simulations across randomly selected conditions.

The effect of $p_{copyActWrong}$ and the presence of frequency dependent effects is further illustrated by analysis of the performance of each strategy by itself. For all melee strategies, single simulations containing only one strategy were run, using the same conditions as in the pair-wise tournament phase. The same simulations were then run again but with $p_{copyActWrong}$ set to zero, and the results compared in terms of the average individual mean lifetime payoff in each population. Under the pair-wise conditions, there was a strong inverse relationship between the mean lifetime payoffs of strategies playing alone and their scores in the tournament melee – lower ranked strategies had higher fitness when playing alone than those ranked higher (Figure 4.4d). The effect of setting $p_{copyActWrong} = 0$ is dramatic for those strategies that rely exclusively on OBSERVE, with the average individual payoffs in populations containing only those strategies dropping to one quarter or less of their previous values. This again suggests that copy error is a significant source of novel behaviour. However, the strategy that ranked 6th, *dynamicAspirationLevel*, while relying heavily on OBSERVE, did not do so exclusively (average proportion of learning moves that were OBSERVE was 0.995 across all melee simulations), and its performance when playing by itself was unaffected by setting $p_{copyActWrong} = 0$; thus in this model relatively small amounts of innovation can bring in enough new behaviour to maintain payoff levels.

The two most successful strategies, *discountmachine* and *intergeneration*, each had unique features: the former had a neural network, which it used to decide between learning and exploiting alternatives, while the latter deployed behaviour designed to pass signals from older to younger agents regarding what should be considered a good payoff. The analyses suggest, however, that it was not these unique features that were crucial to their success, as re-runs of the *random* conditions melee with versions of these strategies coded to remove these unique features produced results identical to the original tournament (Figure 4.11). The role of the neural network in the success of the winner, *discountmachine*, was further investigated by playing it against the version of itself without a neural network across 1,000 random melee conditions. The complete version tended to do increasingly better than the reduced version as p_c increased (linear regression of difference between the scores of the strategies against p_c across 1,000 conditions: $\beta = 1.78$, s.e. = 0.2, $t = 8.97$, d.f. =

998, $p < 0.00001$), indicating that under certain conditions the neural network did make a positive contribution to the strategy's performance.

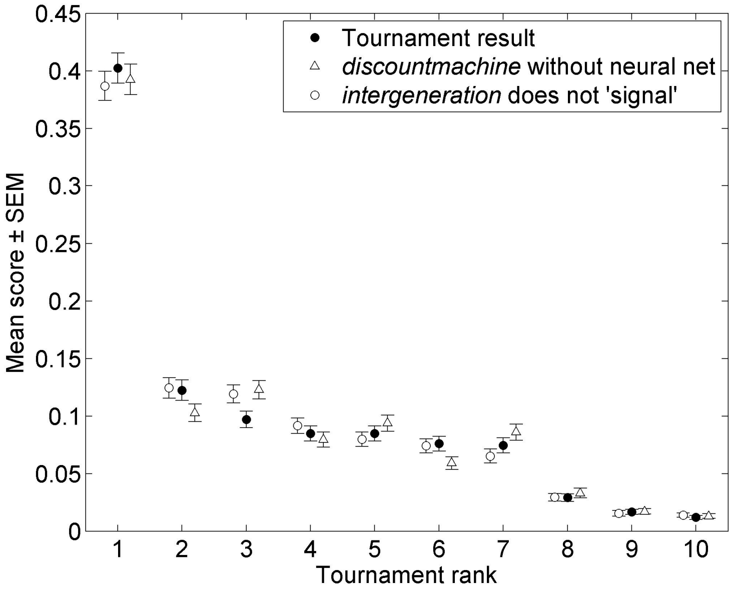

Figure 4.11: Ranked scores from tournament random conditions melee and from runs under the same conditions with the strategies *discountmachine* and *intergeneration* re-coded to remove, respectively, the neural network in *discountmachine* and the attempted intergenerational signalling of *intergeneration*.

OBSERVE moves revealed information about the payoff of behaviour as well as the behaviour. TO examine the implications of this assumption for the tournament results, the random conditions melee was run a further time, devaluing information about social learning payoffs by making payoff observation extremely unreliable (setting sigma, the standard deviation of payoff observation error, to 50, when payoffs themselves are generally in the range 0-50). Under these conditions OBSERVE essentially provided no information about payoff. Nonetheless, while the tournament result is altered in the sense that a different winner emerges, the new winning and second-place strategies, which ranked 4th and 6th in the tournament proper, also use social learning in >95% and >97% of all learning moves respectively (Figure 4.12). Thus the success of social learning in the tournament does not depend on the ability to observe demonstrator payoffs. These are surprising results, given that the error-prone nature of social learning is widely thought to be a weakness of this form of learning, whilst the ability to copy multiple models rapidly or preferentially copy high-payoff behaviour are regarded as strengths (Richerson and Boyd 2005). Strategies relying heavily on social learning did best irrespective of the number of individuals sampled by OBSERVE (Figure 4.7d). These findings are particularly striking in the light of previous theoretical analyses (Boyd and Richerson 1985, Rogers 1988, Feldman *et al.* 1996, Kameda and Nakanishi 2003, Wakano *et al.* 2004, Enquist *et al.* 2007, Kendal *et al.* 2009), virtually all of which have posited some structural cost to asocial learning and errors in social learning. An established rule in ecology specifies that, among competitors for a resource, the dominant competitor will be the species that can persist at the lowest resource level (Tilman 1982). An equivalent rule may apply when alternative social learning strategies compete in a population: the strategy that eventually dominates will be the one that can persist with the lowest frequency of asocial learning (Kendal *et al.* 2009). The tournament findings are consistent with this hypothesis.

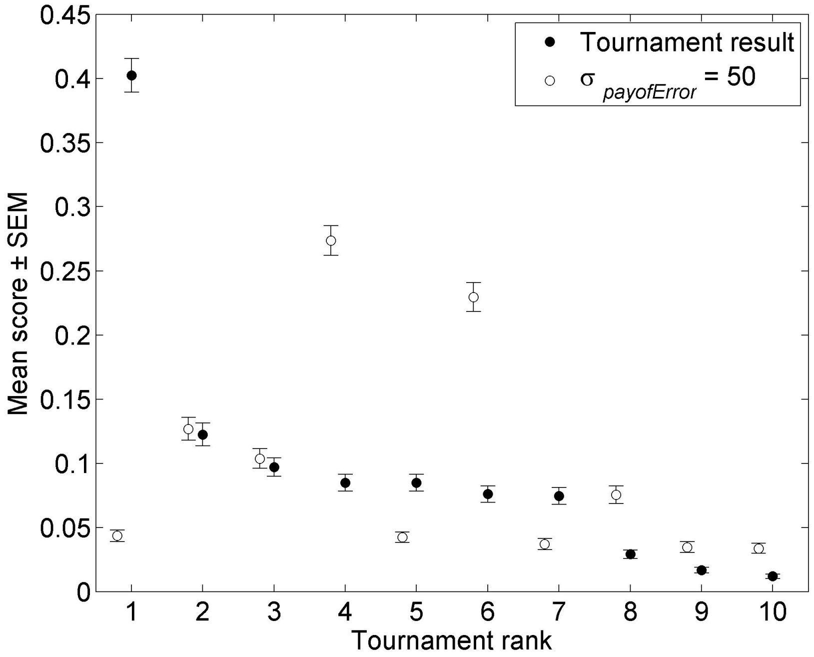

Figure 4.12: Ranked scores from tournament random conditions melee and from runs under the same conditions except with $\sigma_{payoffError}$ set to 50 so as to make the OBSERVE move uninformative with regard to the payoffs of the learned behaviour.

Filtering of adaptive information by demonstrators also underpinned the success of social learning in the tournament. To investigate this an alternative simulation model was run in which OBSERVE returned a behaviour chosen at random from a demonstrator's repertoire with the behaviour the demonstrator had chosen to exploit removed, thereby preventing the filtering of information by rational agents choosing to exploit their best behaviour. A series of such modified simulations were run in which the tournament winner and a version of itself altered to learn only by INNOVATE played against each other, together with the *exploitOneInnovation* strategy used to initiate simulations in the melee phase of the tournament. The rate of environmental change (p_c) across simulations was systematically varied. Five simulations were run at each level of p_c, and the other parameters were fixed at $n_{observe}$=1, $p_{copyActWrong}$=0.05, and $\sigma_{payoffError}$=1, identical to the first phase of the tournament. The results showed that *discountmachine*'s innovating cousin generally dominated the population irrespective of the rate of environmental change (Figure 4.13a). A second analysis, using simulations in which OBSERVE returned a behaviour chosen at random from a demonstrator's repertoire with the behaviour the demonstrator had chosen to exploit retained, also dramatically reduced the range over which social learning prospered, restricting this to highly stable environmental conditions. These results clearly demonstrate that the filtering of information by informed individuals is crucial to the success of social learning. In the absence of this filtering, social learning is in fact costly enough, through its associated errors and propensity to fail to introduce new behaviour to an agent (which occurred at a rate of 53% of OBSERVE moves in the first phase of the tournament), to be selectively disadvantaged.

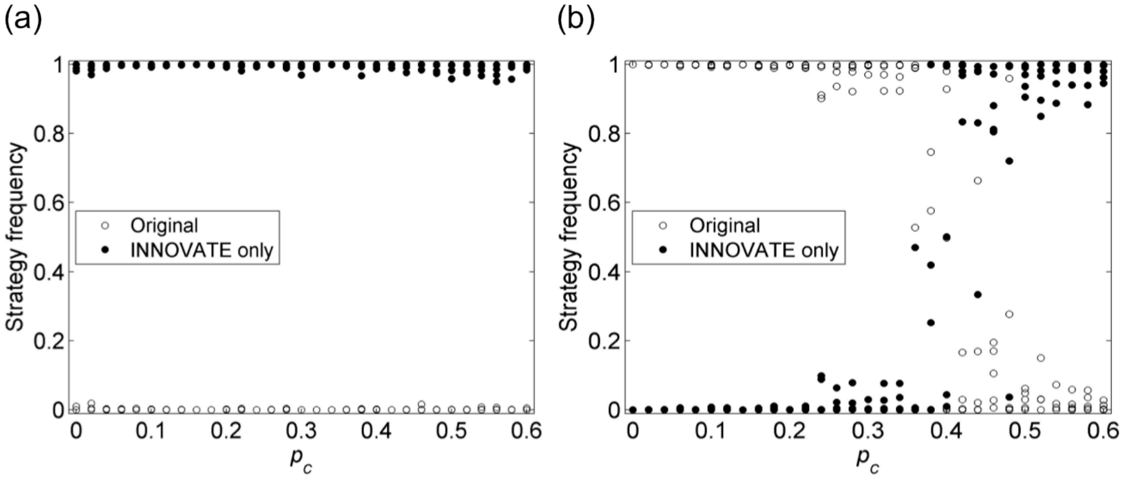

Figure 4.13: (a) Results of a series of simulations in which the tournament winner played against a version of itself altered to learn only by INNOVATE in a model where OBSERVE returned a behaviour selected at random from a demonstrator's repertoire. (b) Results of a series of simulations in which the tournament winner played against a version of itself altered to learn only by INNOVATE in a model where OBSERVE returned no behaviour in the event of a copying error (rather than a randomly selected behaviour as in the original tournament).

DISCUSSION

The most significant outcome of the tournament is the remarkable success of strategies that rely heavily on copying when learning, in spite of the absence of a structural cost to asocial learning, an observation evocative of human culture. This outcome was not anticipated by the tournament organisers, nor by the committee of experts established to oversee the tournament, nor, judging by the high variance in reliance on social learning (Figure 4.8a), by most of the tournament entrants. While the outcome is in some respects consistent with models that used simpler environmental conditions and in which individual learning is inherently costly relative to social learning (Boyd and Richerson 1985), in the tournament the environment was complex and there was no inherent fitness cost to asocial learning. Indeed, there turned out to be a considerable cost to social learning, as it failed to introduce new behaviour into an agent's repertoire in 53% of all the OBSERVE moves in the first tournament phase, overwhelmingly because agents observed behaviours they already knew. Nonetheless, social learning proved advantageous because other agents were rational in demonstrating the behaviour in their repertoire with the highest payoff, thereby making adaptive information available for others to copy. This is confirmed by modified simulations wherein social learners could not benefit from this filtering process, in which social learning performed poorly (Figure 4.13b). Under any random payoff distribution, if one observes an agent using the best of several behaviours that it knows about, then the expected payoff of this behaviour is much higher than the average payoff of all behaviours, which is the expected return for innovating. Previous theory has proposed that individuals should critically evaluate which form of learning to adopt in order to ensure that social learning is only used adaptively (Enquist *et al.* 2007), but a conclusion from the tournament is that this may not be necessary. Provided the copied individuals themselves have selected the best behaviour to perform from at least two possible options, social learning will be adaptive. It is possible that this is the reason why copying is widespread in the animal kingdom.

That social learning was critical to the success of the winning strategy is shown by the results of running the random conditions portion of the second tournament stage with a version of *discountmachine* recoded to learn only by INNOVATE – it came last (Figure 4.4b). It was also shown that *discountmachine* dominated its recoded cousin across a large portion of the plausible parameters space with respect to environmental change (Figure 4.14), with payoffs needing to change with 50% probability per round before the INNOVATE-only version could gain a foothold. This is another way that the tournament challenges existing theory, which predicts that evolution will inevitably lead to a stable equilibrium where both social and asocial learning persist in a population (e.g. Rogers 1988).

It is important to note that, while this tournament may offer greater realism than past analytical theory, the simulation framework remains a simplification of the real world where, for instance, model-based biases and direct interactions between individuals operate (Apesteguia *et al.* 2007). It remains to be established to what extent the results will hold if these are introduced in future tournaments, where the specific strategies that prospered here may not do so well. Nonetheless, the basic generality of the multi-armed bandit problem lends confidence that the insights derived from the tournament may be quite general.

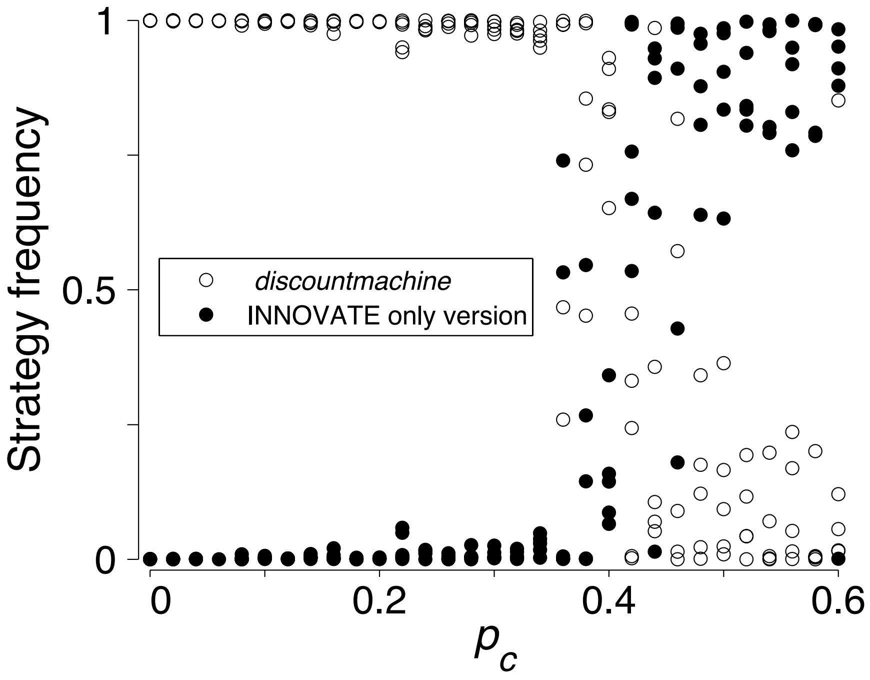

Figure 4.14: Results of a series of simulations in which the tournament winner played against a version of itself altered to learn only by INNOVATE. The rate of environmental change (p_c) was systematically varied. Five simulations were run at each level of p_c. Other parameters were fixed at $n_{observe}$=1, $p_{copyActWrong}$=0.05, and $\sigma_{payoffError}$=1.

The tournament also draws attention to the significance of social learning errors as a source of adaptive behavioural diversity. In the tournament, there was a probability, $p_{copyActWrong}$, that a social learner acquired a randomly selected behaviour rather than the observed behaviour. Modelling social learning errors in this way means new behaviour can enter the population without explicit innovation. The importance of these errors is illustrated by the fact that strategies relying exclusively on social learning were unable to maintain high individual fitness when $p_{copyActWrong} = 0$ (Figure 4.4d). This does not mean that the success of the winning strategy depended on the condition $p_{copyActWrong} > 0$ – in the presence of other strategies providing the necessary innovations, *discountmachine* and *intergeneration* maintain their respective first and second places when $p_{copyActWrong} = 0$ (Figure 4.4c). Other models have highlighted copying errors as potentially important in human cultural evolution (Henrich and Boyd 2002), but the extent to which adaptive innovations actually come about through such errors is an important empirical question ripe for investigation.

The ability to evaluate current information based on its age, and to judge how valuable that information might be in the future, given knowledge of rates of environmental change, is also highlighted by the tournament. There is limited empirical evidence that animals are able to discount information based on the time since it was acquired (Van Bergen *et al.* 2004), but little doubt that humans are capable of such computation. The tournament suggests that the adaptive use of social learning could be critically linked to such cognitive abilities. There are obvious parallels with the largely open question of mental time-travel, the ability to project current conditions into the future, in non-humans (Suddendorf 2007), raising the hypothesis that this cognitive ability could be one factor behind the gulf between human culture and any non-human counterpart (see Chapter 6). A critical next step will be to evaluate experimentally to what extent human behaviour mirrors that of the tournament strategies (e.g. Salganik 2006). By drawing attention to the importance of adaptive filtering by the copied individual and temporal discounting by the copier, the tournament helps to explain both why social learning is common in nature and why human beings happen to be so good at it.

SECTION 2, CHAPTER 5:

HOW COPYING AFFECTS THE AMOUNT, EVENNESS AND PERSISTENCE OF CULTURAL KNOWLEDGE: INSIGHTS FROM THE SOCIAL LEARNING STRATEGIES TOURNAMENT

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INTRODUCTION

Understanding the evolution of human culture is one of the greatest challenges facing science. The gulf between the complexity of human culture and cognition and that observed in other animals is so vast that to many it has seemed unbridgeable. Nonetheless, evolutionary links are there to be found. Most behavioural biologists now acknowledge, for example, the existence of diverse behavioural traditions observed in other apes and monkeys (Emery and Clayton 2004; Sumpter 2006; Conradt and List 2009), the surprisingly complex cognition of corvids (Emery and Clayton 2004), and the impressive collective decision-making and rich social behaviour of insect societies (Sumpter 2006; Conradt and List 2009). Yet the fact remains that however much we talk up these phenomena, there is a chasm between our achievements and theirs. If one accepts the argument that chimpanzees, and for that matter monkeys, whales, birds and fishes, have some semblance of culture, then one must acknowledge that the 'culture' of nonhuman animals is very different from our own.

Such reasoning leads to two kinds of question. First, in what ways do the processes that underlie human culture differ from those observed in other animals, such that they can create such distinct patterns of behavioural, social and technological complexity. Second, how did those processes that underlie human culture evolve out of the kind of rudimentary capabilities observed in other animals? In simple terms, we can ask 'what is the gap?' and 'how can we bridge it?' Here, to answer these questions, this analysis draws on and extends insights into the evolution of culture that emerged from the social learning strategies tournament (see Chapter 4 for a full discussion). The current chapter uses the same model framework to investigate how the strategies that were successful in the tournament affect cultural evolution. Here the analyses of the tournament results discussed in Chapter 4 are extended to consider how the strategies that did well affect the *amount*, *evenness*, and *persistence* of cultural traits.

Amongst the striking differences between human and animal culture is the sheer amount of culture that humans possess. Here, the *amount* of culture refers to the number of cultural traits that a population knows about, or actually expresses in behaviour, which are labelled the amount of knowledge and behaviour respectively. This analysis investigates the relationship between these quantities and the learning strategies deployed in a population, expressed as the amount and type (social or asocial) of learning used.

Using the tournament structure it is also possible to investigate how evolutionarily successful strategies affect the *evenness* of culture, which is defined here as the flatness or uniformity of the distributions of knowledge and expressed behaviour across a population. Logic suggests that copying should increase the behavioural evenness exhibited by a population, since copying generates homogeneity in exhibited behaviour, but it is less clear whether and how copying will affect the evenness of acquired knowledge.

Finally, this chapter looks at how these strategies affect the *persistence* of cultural traits, which is defined here as the average length of time individual traits persist, given that they became known or expressed by at least one individual, either in the knowledge or the expressed behaviour of at least one individual in a population. Human culture is uniquely cumulative, with each generation building upon the cultural knowledge of the previous generations (Tomasello 1994). Cumulative culture requires cultural traits to persist for long enough to allow refinements or elaborations of acquired knowledge (Enquist *et al.* 2010). The cultures of other animals are frequently characterized by ‘lightning traditions’, which rapidly sweep through a group of animals, and then are replaced as quickly, with little sign of any accumulation of knowledge (Laland *et al*. 1993). Conversely, humans today possess knowledge first acquired many thousands of years ago. It is plausible that the preservation of acquired knowledge over long periods of time creates the opportunity for refinement, elaboration and diversification (Enquist *et al*. 2010; Lewis and Laland *in press*), and that this again explains some of the uniqueness of human culture. The data generated by the tournament can be used to explore how the proportion of learning moves that is OBSERVE affects the longevity of cultural knowledge. The analysis considers how the level of copying affects the average persistence of both exploited behaviour and behavioural knowledge in the population’s repertoire.

One of the challenges facing a developing theory of cultural evolution is to link the small-scale, social learning decisions of individuals to the creation and subsequent evolution of the collections of knowledge, tradition, language and behaviour that characterize populations. The tournament is effective both because it proposes specific means by which copying may be implemented strategically to enhance copying efficiency, and because it illustrates the population-level consequences of such strategies. The sections below first summarise the methods and findings of the social learning strategies tournament then present analyses of tournament simulations designed to shed light on how copying affects the longevity, evenness and amount of cultural knowledge in the virtual ‘cultures’ constructed by the strategies that did well in the tournament. Finally, these insights are collated to shed light on both the field of cultural evolution and, more generally, understanding of the evolution of culture.

THE DYNAMICS OF CULTURAL KNOWLEDGE AND BEHAVIOUR: FACTORS AFFECTING AMOUNT, EVENNESS AND PERSISTENCE

Methods

The tournament was run as described in detail in Chapter 4. The initial tournament analysis (Chapter 4) focussed primarily at the individual level, asking how and why individuals using certain strategies performed well. However, the tournament framework also allowed us to explore factors such as how copying affects the amount of cultural knowledge at the population level. Each simulation contained 100 individuals; each of those individuals has, at any one time, a set of behaviour patterns in its repertoire (almost always a subset of the 100 possible behaviour patterns defined in the multi-armed bandit). These combined repertoires thus constitute the combined knowledge of that population. The population can also be characterised by the set of behaviour patterns it is performing, provided at least one individual is playing EXPLOIT at a given time. This distinction between things individuals know about and things individuals actually do, between knowledge and behaviour, is not often captured in theoretical studies of cultural evolution, and cultural evolution theory has been criticised precisely for this reason (Cronk 1995). It is however a core feature of the tournament model that behaviour and knowledge can be distinguished. Here these two aspects of culture are investigated independently, by using simulations that keep track of three simple measures characterising the knowledge and behaviour present in these virtual cultures.

The first quantity tracked was simply the number of different behaviour patterns present, which was expressed as a proportion of the 100 possible behaviour patterns defined by the multi-armed bandit. Both the proportion (out of 100) of possible behaviour patterns that were known – i.e. that were present in the repertoire of at least one individual – and the proportion that were actually performed in an EXPLOIT move by at least one individual were measured. These proportions were labelled the *amount* of knowledge and *behaviour* respectively; they measure the number of behaviour patterns known about, or performed, by a population at a given time.

Second, to describe what is here termed *evenness* in the context of this paper, the flatness of the frequency distribution of behaviour patterns across the population was measured using Pielou's evenness index (Smith and Wilson 1996). This is a measure used in quantifying species evenness in ecological communities based on the Shannon-Wiener diversity index, and is given by

$$J = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln(S)} , \qquad (5.1)$$

where S is the number of species present in a sample, and p_i is the relative frequency of species i in the sample. In this case, it is used as a measure of the distribution of behaviour patterns, so S is the number of possible behaviour patterns (100) and p_i is the number of individuals in the population at that iteration with that behaviour. The value of J can range from 0 to 1, the latter representing maximum evenness. For example, consider a sample of 100 individuals, in an environment where 5 behaviour patterns were possible. Maximum evenness would be if twenty individuals each performed one behaviour (p = [0.2 0.2 0.2 0.2 0.2], J = 1), while minimum evenness would be if 100 individuals performed one behaviour and none performed the others (p = [1 0 0 0 0], J = 0). An uneven distribution of behaviour with most individuals choosing the same behaviour could come about through conformism, the strategy of preferentially copying the most commonly seen behaviour, the importance of which in human culture is an area of active debate (Eriksson *et al.* 2007; Henrich and Boyd

1998). This analysis was used to explore the extent to which apparently conformist outcomes, such as an uneven distribution of behaviour, could arise in the absence of explicitly conformist strategies being deployed by individual agents (Franz and Matthews 2010).

Finally, the rate of cultural turnover was investigated by calculating what was termed the *persistence* of knowledge and expressed behaviour. Persistence was the average number of iterations that behaviour patterns were known (as before, present in the repertoire of at least one individual) or for which they were performed (as before, being chosen in an EXPLOIT move by at least one individual), given that they had become known or expressed by at least one individual (such that a persistence value of zero did not occur).

The analysis was concentrated on the top ten strategies (Figure 4.4a) as, being highly effective, it was reasoned that of the strategies considered these are most likely to occur at high frequency in nature and so it is their behaviour that is of greatest relevance here. Data was gathered on amount, evenness and persistence by running two batches of tournament simulations. The first re-created the *random melee* section of the tournament, where the top ten strategies competed simultaneously across varied simulation parameters, to investigate how variation in learning strategies affects cultural dynamics. Varying simulation parameters reflect different assumptions about the environmental conditions. The cultural measures that were analysed could change in response to this variation through both the way strategies themselves changed their behaviour in response to varying parameter values, and also the way in which the parameter values themselves altered the simulation dynamics by changing the error rates and relative cost associated with social learning. The second set of simulations took each strategy in turn and ran simulations with only that strategy present, using the same parameter values as the *pairwise* tournament phase (Chapter 4).

This exercise was repeated twice, in each case a major alteration was made to the model assumptions. First, the probability of copying the wrong behaviour when playing OBSERVE was set to zero ($p_{copyActWrong} = 0$), removing the assumption that copying errors could introduce new behaviour into a population. Second, the standard deviation of a normally distributed error applied to payoffs returned by OBSERVE was set such that $\sigma_{\text{copyPayoffError}}$, = 100, making information about the payoffs of behaviour acquired by social learning too inaccurate to be useful. The characteristics of the virtual cultures constructed by the single strategies under these varied assumptions were compared.

Results

It is worth noting that this was not a standard simulation study in which one changes a parameter to analyze how this parameter causally affects some measure in the results, rather it was a correlation study, where both dependent and independent variables were outcomes of variation in other variables. Several noteworthy results emerged. The learning approach of the mixed strategy populations were first characterised simply as the average proportion of learning in each round that was social (i.e. the number of individuals playing OBSERVE divided by the number of individuals playing either learning move – OBSERVE plus INNOVATE), how this single feature affected the population level measures described above was then examined (Figure 5.1). In general, it was found that there was a step change in the relationships examined, which for the parameter sets explored, occurred after the proportion of OBSERVE exceeded around 0.7.

High levels of social learning were associated with increased amounts of knowledge until the proportion of OBSERVE exceeded ~0.7, after which there was a ceiling effect with populations generally knowing all possible behaviour patterns (Figure 5.1a). This is a counter-intuitive result because, compared to reliance on asocial learning, a reliance on social learning must reduce the amount of new information entering a population (see Chapter 2 for example). This apparent paradox results in part from the assumption that copy error could introduce new behaviour into a population, hence more social learning leading to more copying errors leading to more knowledge, an interpretation which is supported by the results of switching off copying errors, presented below. More copying also means that behaviour patterns are more likely to be retained within the population, since multiple copies of any given variant are more likely to be generated. Under restricted circumstances, this can increase the amount of cultural knowledge in the population, where the knowledge that is built up over time is not lost (Figure 5.1e) and compensates for the reduced introduction of variants that would have occurred through innovation. However, for increases in copying to be associated with increases in the amount of culture there has to be a source of new variants, either stemming from innovation or copy-error.

Conversely, high levels of social learning were associated with reduced numbers of expressed behaviour patterns, especially when the proportion of OBSERVE exceeded ~0.7 (Figure 5.1b). Accompanied by the concurrent reduction in the evenness of behaviour apparent in Figure 5.1d, this observation suggests that in populations containing effective strategies and with high levels of social learning, individuals concentrate on performing relatively few behaviour patterns even though they have knowledge of many. Those few behaviour patterns performed are drawn from those with the best payoffs available at that time as many individuals choose to adopt them.

As these patterns in the amount of culture were counter-intuitive, it was important to ask whether they could be explained either by simply the amount of learning that strategies did (quantified as the proportion of moves that were either OBSERVE or INNOVATE), or directly by the variation in simulation parameter values. Simple GLMs were fitted with identity link and normal error (Faraway 2006) to the data on the amount of knowledge, using as predictors the average proportion of learning in each simulation, which is termed p(learn), and the values of the four simulation parameters (p_c, $n_{observe}$, $\sigma_{copyPayoffError}$, and $p_{copyActWrong}$).

These predictors, including all first-order interactions, were used in a model selection analysis, testing all possible combinations to see which gave the best fit, as determined by the lowest Akaike Information Criteria (AIC) value. Once the best model had been identified, AIC was then compared with that of an identical model but with the average proportion of learning that was social (which is termed p(OBSERVE)) as an additional predictor. The best model without p(OBSERVE) contained all predictors and interactions save $\sigma_{copyPayoffError}*p_{copyActWrong}$ and $\sigma_{copyPayoffError}*p$(learn), with an AIC of -7013.5. The same model with p(OBSERVE) added as a predictor had an AIC of -7093.4, some 79.9 units smaller, comfortably exceeding 3, the rule of thumb generally used to indicate a better fitting model (Burnham and Anderson 2002). This analysis shows that while other factors certainly had an effect, the proportion learning that is social still independently explains a significant amount of variation in the amount of knowledge.

High levels of social learning did not affect the evenness of knowledge (Figure 5.1c), but drastically reduced the evenness of behaviour (Figure 5.1d). Once the proportion of OBSERVE exceeded ~0.7 populations emerged in which most individuals performed just one or two behaviour patterns.

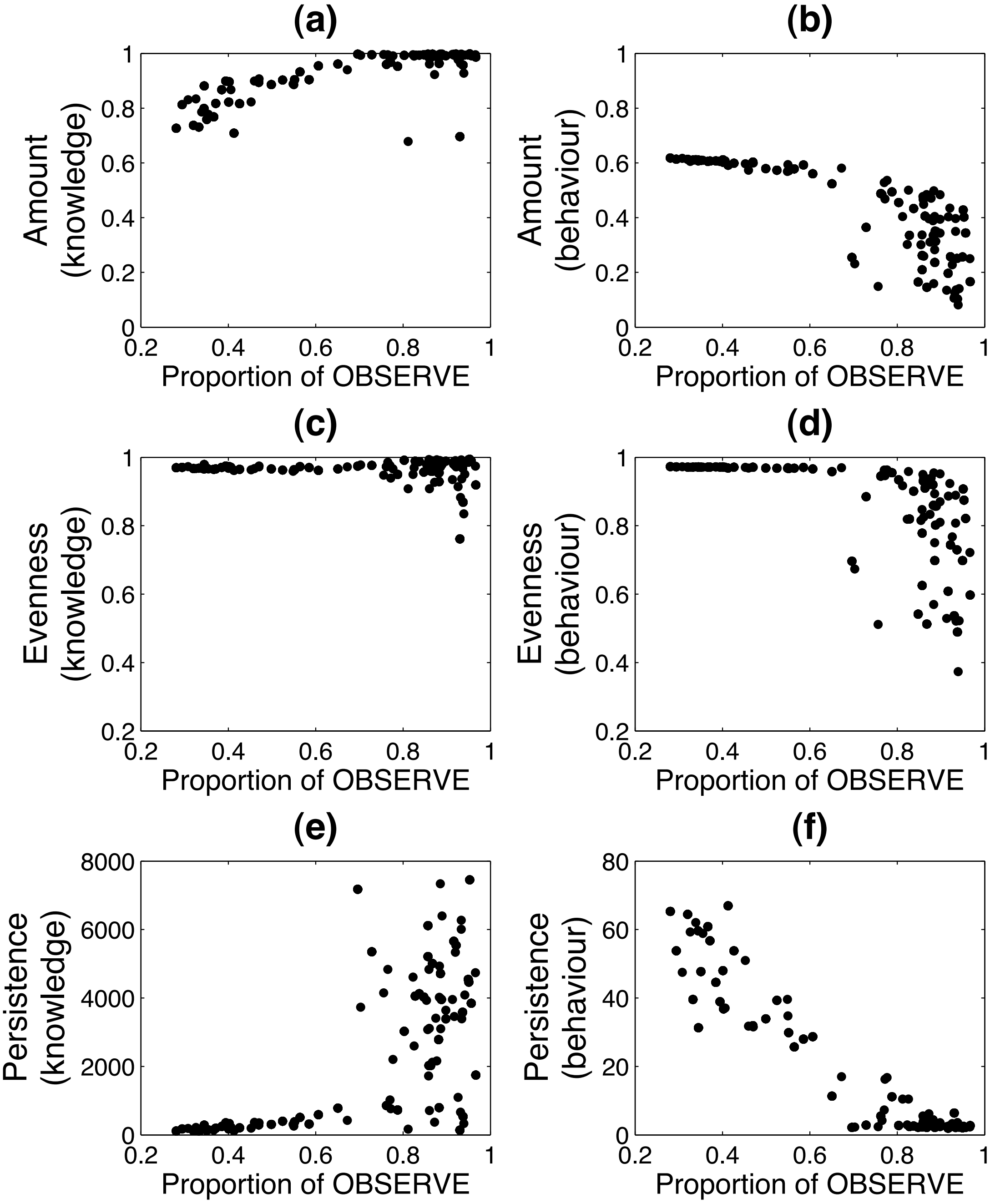

Figure 5.1: How effective learning strategies affect culture at the population level. Plots show quantitative measures of the (a-b) amount, (c-d) evenness, and (e-f) longevity of knowledge (a,c,e), and behaviour (b,d,f), plotted against the proportion of learning that was social, in mixed-strategy populations running under the *random melee* tournament conditions. Each point represents the average value across all iterations for a single 10,000-iteration simulation run. Note the order of magnitude difference in y-axis scales between (e) and (f).

High levels of social learning (especially >~0.7) were sometimes associated with very large increases in the persistence, or longevity, of knowledge in these populations (Figure 5.1e). Given that the average lifespan of individuals in these populations is 50 iterations, it is clear that increased levels of social learning can, in this model, lead to knowledge that far outlives its original innovators, lasting for tens and sometimes hundreds of generations. Conversely, in populations with high levels of social learning persistence of behaviour was reduced, because effective strategies were quick to stop exploiting behaviour that did not return payoffs as high as expected, leading to a low average persistence (as the most effective strategies were the ones that did most social learning, populations with high levels of social learning are likely dominated by those strategies).

It emerged that only the evenness and amount of behaviour (not knowledge) were affected by varying the simulation parameters (Figure 5.2), while persistence was not affected at all and that increased rates of environmental variation were associated with both greater evenness and more expressed behaviour patterns (Figure 5.2a,c), even though the evenness and amount of knowledge were not affected. It is not inevitable that an increased amount of expressed behaviour is linked to increased evenness – it would be perfectly possible, for example, for a population to contain one very popular behaviour and a lot of relatively unpopular ones – but in these simulations they do appear to be linked, a result of individuals diverging in their estimates of what is currently the best behaviour to be deploying. Surprisingly, the extent to which social learning was error-prone appeared to have no effect on knowledge and behaviour at the population level (Figure 5.2b,d), even when it reached extreme levels such as 0.5.

How two important assumptions affected the outcome of the tournament was also investgated. These assumptions were first, that social learning carries a probability of learning the wrong behaviour (copy error) and thereby introduces new knowledge into a population, and second, that social learners are capable of learning the payoff associated with a given behaviour (payoff information). It is easy to envisage situations where these might not apply – for example, in the first case where strict error correcting mechanisms are deployed to maintain fidelity (reproduction of classical music, or ballet steps), and in the second case, when the behaviour is one with delayed or opaque payoffs (e.g. planting seeds). Simulations containing single strategies explicitly were run to consider the effect of no copy error and no payoff information (Figure 5.3).

These factors had strong effects on the amount of behaviour and knowledge. Both were reduced in the absence of copying errors but increased in the absence of useful payoff information (Figure 5.3). They had either no effect (in the absence of copy error) or relatively little effect (in the absence of payoff information) on the evenness of either behaviour or knowledge, except that a lack of payoff information slightly increased the evenness of both knowledge and behaviour. Switching off copy error profoundly affected the persistence of behaviour, increasing it up to seven-fold for some strategies, but did not affect the persistence of knowledge. A lack of payoff information appeared to have little general effect on persistence, although in some strategies it appeared to increase the persistence of knowledge. These effects are generally intuitive. The switching off of copying errors reduces the supply of new information into a population when that population learns mostly by social learning, which is thought to be an important weakness of social learning in general (see Chapters 2 and 4), resulting in reduced amounts of knowledge and behaviour.

Individuals in these populations were forced to rely heavily on that reduced set of behaviour patterns they did know about, resulting in an increased persistence of behaviour in a population. Finally, increased evenness of behaviour in the absence of payoff information likely reflects a reduced ability by the strategies in question to identify the currently optimal behaviour.

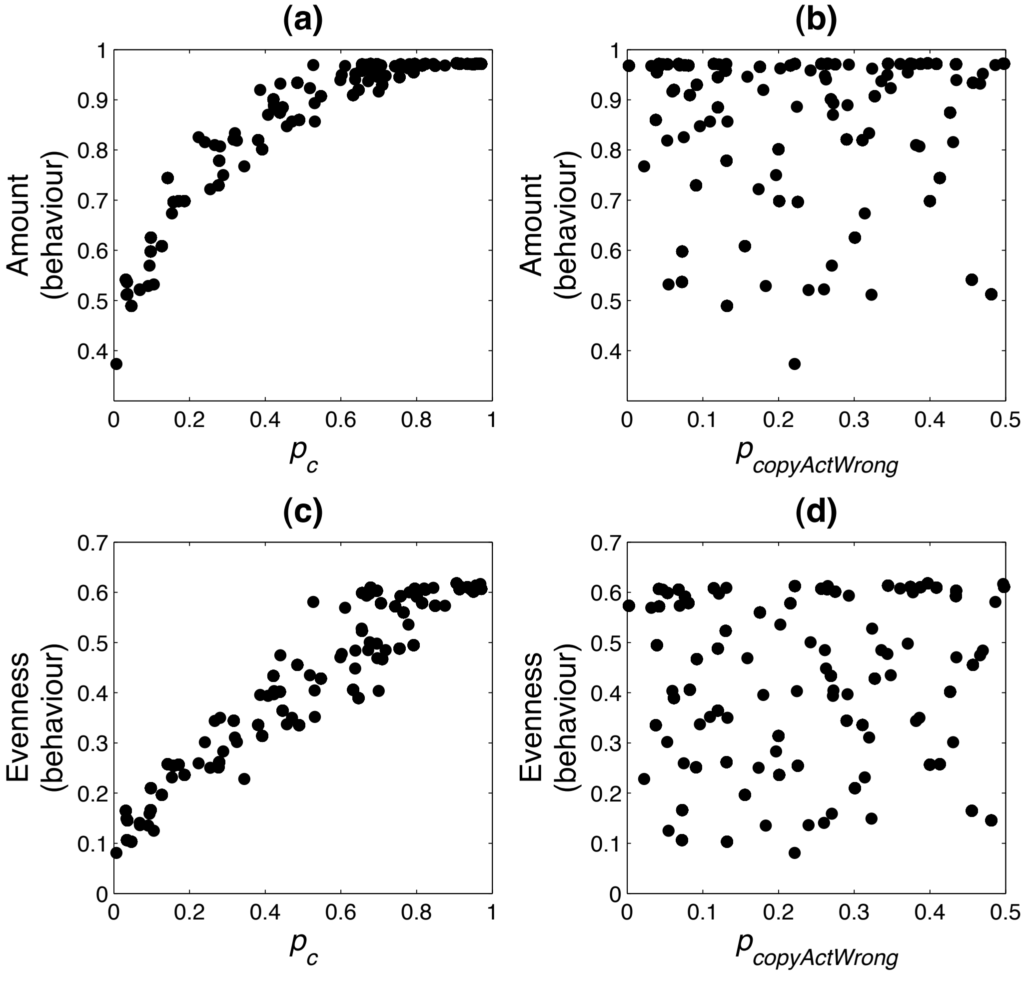

Figure 5.2: How the rates of environmental change and copying error affect the amount and evenness of expressed behaviour when effective strategies are present. Plots (a-b) show the proportion of the 100 possible behaviour patterns being used (i.e. by playing EXPLOIT), in mixed-strategy populations running under the *random melee* tournament conditions, as a function of (a) the rate of environmental change, and (b) the standard deviation of error in the estimated payoff of a behaviour learned socially (i.e. by OBSERVE). Plots (c-d) show the evenness of the distribution of behaviour patterns being used, in the same populations, as a function of (c) the rate of environmental change, and (d) the standard deviation of error in the estimated payoff of a behaviour learned socially. Each point represents the average value across all iterations for a single 10,000-iteration simulation run.

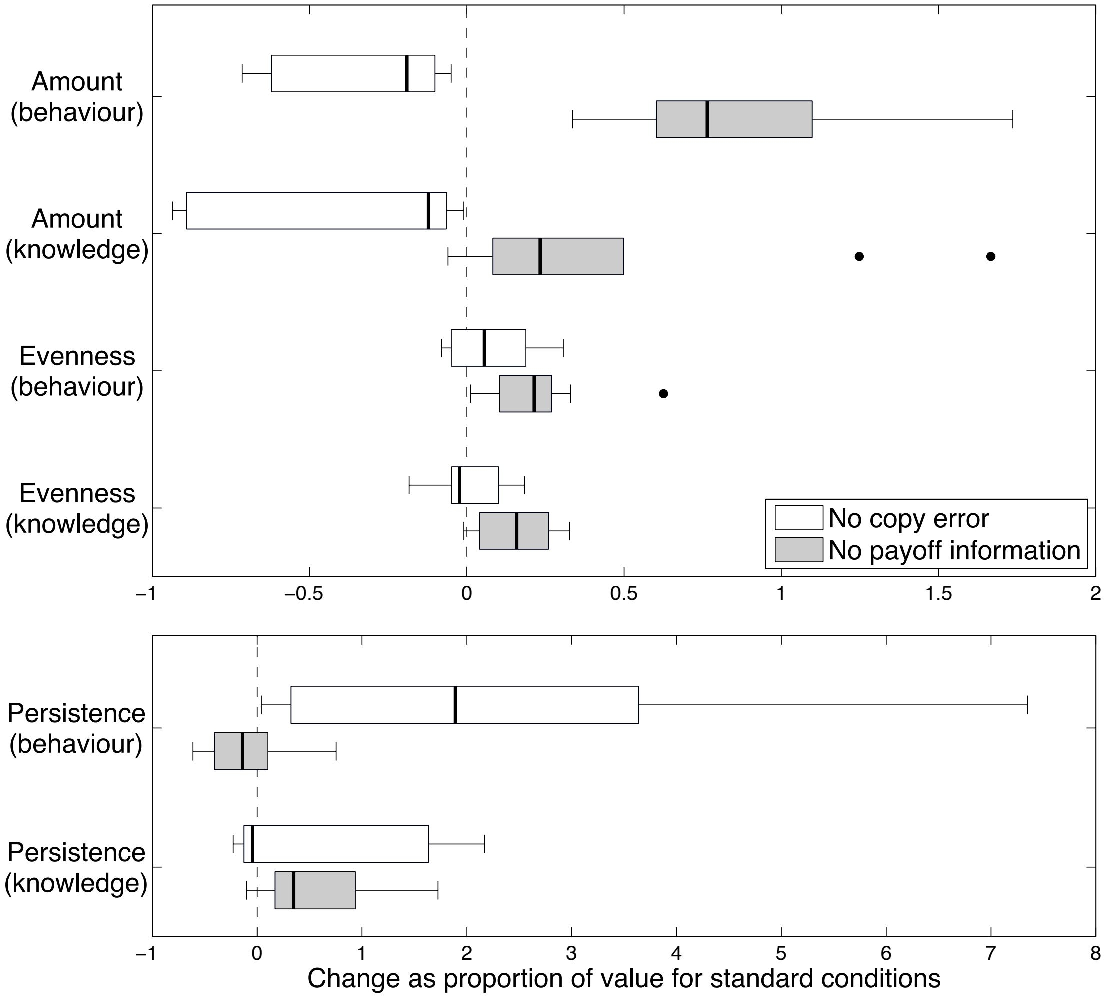

Figure 5.3: The effect of information transmission parameters on (top panel) amount, evenness and (bottom panel) persistence of knowledge and behaviour (note differing x-axis scales between panels). Boxplots show the change from the standard conditions used in the tournament when (white bars) the probability of copying the wrong behaviour when playing OBSERVE, $p_{copyActWrong} = 0$ or when (grey bars) the social learning of payoffs is so error-prone as to be uninformative (the standard deviation of a normally distributed error applied to payoffs returned by OBSERVE, $\sigma_{\mathrm{copyPayoffError}} = 100$). Values are taken from averages over ten 10,000 iteration simulations in each of which only one of the ten best tournament entries was present.

DISCUSSION: WHAT DOES THE TOURNAMENT IMPLY FOR CULTURAL EVOLUTION?

Analysis of the social learning strategies tournament (Chapter 4) revealed that social learning is a more effective means of knowledge gain than asocial learning under most biologically plausible conditions, even when it is highly error prone. Copying pays because the copied individual is usually rational in performing his or her most effective (i.e. highest-payoff) behaviour, such that only the subset of high-performance behaviour patterns are exploited, thereby inadvertently filtering behaviour for the copier. This is probably why copying is widespread in nature, since even random copying is more effective than trial-and-error learning, and effective copying can be performed in the absence of cognitively challenging learning rules. However, this does not detract from the utility of strategic copying. The most successful strategies were highly selective about when they copied, which they achieved by engaging in bouts of copying only when payoffs dropped significantly, and evaluating information based on its age. It was only when copying was conducted in this efficient manner that it increased mean fitness within the population. This may explain why a reliance on social learning has led to demographic success in humans but not in other animals; conceivably, only we copy with sufficient efficiency and fidelity to give the demographic success observed in human history (Boyd and Richerson 1985).

The analyses of population level cultural characteristic produced a number of interesting insights. Humans possess a great deal more cultural knowledge than other animals and this analysis suggests that this may go hand-in-hand with our greater reliance on social learning compared to other animals. The results outlined in this chapter were consistent with this hypothesis and established a positive relationship between the proportion of learning that was OBSERVE and the amount of cultural knowledge in the population (Figure 5.1a). While, in principle, this relationship need not be a causal one, the aforementioned analyses show that it probably is: that is, that under restricted circumstances increased reliance on copying can increase the amount of culture present in the population through retaining knowledge. However, it is not possible to rule out the idea that the relationship between *p*OBSERVE and amount of knowledge is partly a product of selection between alternative strategies, perhaps favouring strategies associated with large repertoire sizes. Learning strategies can also be characterised by the amount of learning they do, and the statistical analyses presented here showed that this also affected the amount of culture present in a positive way, which is an intuitive result, but that this factor on its own was a much less powerful predictor of the data than the proportion of social learning, which is perhaps less intuitive. High levels of copying were associated with complete knowledge saturation, such that all theoretically possible behaviour was represented in the repertoire of at least one individual in the population. This knowledge was retained in spite of the fact that enhanced copying led to a much smaller average proportion of behaviour actually being expressed at any point in time (Figure 5.1b).

These results are perhaps best understood in conjunction with the striking effect of copying on the retention of knowledge within a population (Figure 5.1e). A heavy reliance on social learning led to an average duration of knowledge within populations that was several orders of magnitude longer than for populations reliant on asocial learning. There was a threshold level of copying, above which cultural knowledge could be retained for many hundreds of generations (given an average lifespan of 50 iterations). It is possible that it is this retention of knowledge that allows knowledge repertoires to approach saturation when populations rely heavily on social learning, because even with very low levels of innovation, if knowledge persists then it will over time accumulate. The caveat here is that there must be a source of new variation present, either copy-error or occasional innovation. Once again, there is a marked contrast with the strong negative effect of copying on the persistence of behaviour (Figure 5.1f). High levels of copying led to rapid turnover in the behaviour patterns exploited, without a concurrent loss of knowledge from the population's repertoire. These observations have parallels in human populations, where we simultaneously witness fads and fashions that change rapidly, representing high turnover in behaviour, and the retention of cultural knowledge over millennia. By illustrating how copying enhances the persistence of knowledge, this analyses explain why these observations are not conflicting.

These observations help to resolve the conundrum that, while logic dictates that copying promotes behavioural homogeneity, humans have accumulated large amounts of cultural knowledge. As expected, individuals converge, through copying, on high-payoff behaviour, such that increasing levels of copying reduce the proportion of behaviour exploited to the high-performance end of the spectrum. However, in a changing environment, with individuals born naïve, inevitably there is some low-level exploitation of poor-performing behaviour too. It would seem that copying sometimes promotes the maintenance of cultural knowledge in a population, by preventing such knowledge from being lost when individuals die. This illustrates, once again, the striking adaptive advantages of social learning: individuals rapidly converge on, and reap the benefits of, exploiting high-payoff behaviour, yet at the same time high-copying populations retain high levels of cultural knowledge, conferring the plasticity to switch behaviour when environments change.

As expected, the analysis also found that copying typically reduced the evenness of exploited behaviour, because it leads to a small number of high-performance behaviour patterns being disproportionately performed (Figure 5.1d). Indeed, even in the absence of an explicit ‘conformist learning’ rule being deployed by individual agents, there was some semblance of conformity emerging at the population level, reflected in lower evenness of the distribution of behaviour (Figure 5.1d) a finding consistent with other analyses (Matthews *et al* 2010). This did not, however, greatly affect the size of the cultural knowledge base (Figure 5.1a), since, as described, it allowed more knowledge to be retained over a greater period. The tournament simulations focused on a single focal population, and it is possible that, were multiple populations involved, the large cultural knowledge base promoted by copying would lead to extensive cultural diversity between populations.

One of the cleanest and most intuitive relationships shown by this analysis was between the rate of environmental change and amount of culture, where greater rates of turnover in the environment led to a greater range of behaviour patterns being performed (Figure 5.2a). High rates of change also resulted in more even distributions of behaviour, as no single high-performance behaviour was persistently optimal in the changing world (Figure 5.2c). Unlike much previous theory, which has suggested that a reliance on social learning can sometimes hinder the adaptive tracking of temporally changing environments (Rogers 1988; Feldman *et al*. 1996; Boyd and Richerson 1988b), a heavy reliance on social learning did not compromise the ability of agents in the tournament to adjust to changing environments. This probably reflects the greater biological realism of the tournament over analytical models, since only in the former do individuals possess a repertoire of behaviour. Possessing knowledge of multiple behaviour patterns allows individuals to switch rapidly to an alternative high-performing action when changes in the environment reduce the payoff to the current behaviour. This flexibility dramatically reduces the costs of copying.

Perhaps surprisingly, copy error had little effect on the amount of expressed behaviour (Figures 5.2b and 5.2d), except at the extreme where there was no copy error at all (Figure 5.3). Error-free copying reduced the amount of both cultural knowledge and behaviour, since new behaviour could no longer be introduced by this route. While it is no surprise that without copy error behaviour patterns persisted for longer (Figure 5.3), it is less intuitive that this would lead to individual actions being exploited for longer (on average, twice as long). This reflects the fact that a great deal of copying (53% of all OBSERVE moves in the first tournament phase) failed to introduce new behaviour into individuals' repertoire, as individuals observed behaviour patterns that they already knew about. In the tournament, copy error increases the chances that individuals will acquire new behaviour when they play OBSERVE. These findings reinforce the view that copy error may be an important source of adaptive variation within natural populations (Henrich and Boyd 2002).

One of the more surprising findings from the tournament was that copying paid even when copiers had no information about the payoff associated with the copied behaviour (Chapter 4). In keeping with other researcher (Schlag 1998), it seemed safe to assume that one advantage to copying would be that it allowed individuals to home in on high-performance behaviour; and indeed, this assumption may yet be correct. However, copying offers advantages over trial-and-error learning even if observers receive no payoff information, because even blind copiers benefit from the aforementioned filtering of behaviour by the copied agents (Boyd and Richerson 1985). This insight could help explain the extreme reliance of children on imitation, leading them faithfully to copy even superfluous actions in a demonstrated task. When children copy adults, they are typically taking advantage of decades of information filtering by the adult, making it on average simply more efficient to take their word for it. In the absence of payoff information, greater amounts of cultural knowledge are retained and exploited (Figure 5.3), since the potential to be selective in the acquisition and performance of behaviour is reduced by a lack of payoff information. This also leads to greater evenness in behaviour across the population.

These observations suggest that copying confers an adaptive plasticity on cultural populations, allowing them to respond to changing environments rapidly by drawing on a deep knowledge base. In biological evolution the rate of change is positively related to genetic diversity (Fisher 1930), and formal analyses suggest a similar relationship between the rate of cultural evolution and the amount of cultural variation (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). Accordingly, populations heavily reliant on culture could rapidly diverge behaviourally, exploiting the rich levels of variation retained in their knowledge base. The tournament suggests that the ecological and demographic success of our species, our capacity for rapid change in behaviour, our cultural diversity, our expansive knowledge base, and the sheer volume of cultural knowledge we exhibit, may all be direct products of the heavy, but smart, reliance of our species on social learning.

SECTION 2, CHAPTER 6:

MENTAL TIME TRAVEL, MEMORY AND THE SOCIAL LEARNING STRATEGIES TOURNAMENT

Material from this chapter has been published as:

Fogarty, L., Rendell, L. & Laland, K.N., Mental time travel, memory and the social learning strategies tournament, *in press Learning and Memory*

INTRODUCTION

Learning and memory are two clearly related concepts, with the ability to learn resting on the ability to form memories of past actions. Learning is generally defined as an extended and long-term process whereby an individual can alter its behaviour and state of knowledge, based, in part, on their previous experiences. As the neural substrate for learning, memory can be considered to be a description of how changes in knowledge state, motor abilities or behavioural repertoire are encoded in the brain and later retrieved to form the basis of behavioural changes (Richter 1966). It is therefore not a huge leap in imagination to glean information about memory use from models of learning. Here a short analysis extending those presented in Chapters 4 and 5 is presented paying special attention to the role of memory in the learning exhibited in the social learning strategies tournament.

The strategies submitted to the tournament varied substantially in their performance, affected by a number of factors, the majority of which we will not consider in this chapter (but see Chapter 4). However, the winning strategy, called *discountmachine* submitted by Dan Cownden and Tim Lillicrap, appeared to enhance its performance through a simple form of 'mental time travel', as did several other successful strategies. This chapter discusses what this use of a type of 'mental time travel' by a number of the strategies submitted to the tournament might imply about memory in a social learning context.

Typical definitions of mental time travel involve 'episodic memory' of the past, consideration of the future and an understanding of how these related to the self (Tulving 1983; Suddendorf and Corballis 2007; Dudai and Carruthers 2005). Thus, mental time travel involves subjective reconstruction or construction of past or future events. In the case of humans, researchers can clearly see and demonstrate the presence of episodic memory and future planning. Conversely, in the case of animals, who are unable to verbalise their experiences of memory, researchers must rely on their actions to draw conclusions about the content of their memories and the mechanisms by which they access that content. This has led to the use of the terms ‘episodic-like memory’, ‘future planning’ or ‘*what, where, when*’ (*www*) memory in discussions of animal mental time travel (Clayton and Dickinson 1998; Raby *et al.* 2007; Clayton *et al.* 2003).

The importance of mental time travel and its specificity to humans has been hotly debated for some years (Clayton *et al.* 2003; Suddendorf and Busby 2003; Suddendorf and Corballis 2007). Even in the midst of this debate, it is useful and interesting to examine the effects of memory, and future projection, on the success of individuals in a changing environment. Here it is possible to take a general definition of ‘mental time travel’ and apply it to the tournament strategies. The intention is to elucidate the effect of memory use on the success, or otherwise, of individuals using these strategies. The tournament provides a unique opportunity to examine the effects of different memory use capabilities on evolutionary success in a standardised and simplified environment.

When discussing memory in computer models such as the tournament, we encounter a series of definitional problems that need addressing before proceeding. Each agent in the tournament had full access to their past moves and the results of those moves. In essence the agents had access to what Tulving (1983) called ‘memory as a warehouse’. Therefore, if they chose to, they could remember every move they made from the moment of their birth to their last simulation round. However the agents did not have access to the computer memory containing information about other agents’ histories or environmental parameters.

The agents in the tournament were incapable of the type of complex mental task, vividly reliving the past and imagining the future, described above, making it challenging to define the type of memory to which agents in the tournament model had access. What is seen when looking at these computer agents is how the information encoded in their simple memories can be used (for instance, by weighting more recent learning more heavily than older knowledge, or making predictions into the future about the likely success of cultural behaviour), and what effect the extent to which they access this information can have on the agent's success. Here the analyses are narrowly focussing on personal *www* memory, but since there is no spatial context in the simulations reported here, the 'where' aspect is ignored. The difference between mental time travel and *www* memory is really a difference in subjective experience, say the difference between remembering the time, date and location of your birth and being able to mentally relive the event itself (Suddendorf and Busby 2003). Thus the analysis concentrates on the content of memories rather than the subjective experience of them. This is true for many computer models of learning, which focus primarily on what information is retained and the origins of the information - what individuals learn and from whom. As a result the models are generally agnostic as to the exact memory mechanisms used to encode the information. It is therefore possible to discuss the effects of learning and memory without defining the memory mechanisms in detail.

THE TOURNAMENT

Competitors entering the tournament were asked to specify the circumstances under which individual agents should learn asocially (INNOVATE), learn socially

(OBSERVE), or perform an act from their repertoire (EXPLOIT). These rules were subsequently translated into computer code.

The simulation model was organized into a series of iterations, or rounds. Each round a new entry was made in the memory matrix (termed '*myHistory*') of each agent in the simulation, whose first row contained the round number or age of the agent, second row contained the previous moves (OBSERVE = 0, INNOVATE = -1, EXPLOIT > 0), third row contained the acts learned or exploited, and whose final row contained the payoffs associated with those acts. For example the agent with the following *myHistory*matrix,

$$myHistory = \begin{bmatrix} 1 & 2 & 3 & 4 \\ 0 & -1 & 2 & 2 \\ 3 & 33 & 5 & 8 \\ 6 & 9 & 3 & 1 \end{bmatrix},$$

is four rounds old, played OBSERVE in the first round, learning act 3 with payoff 6 etc.

The tournament was run in two stages, although only the results of the first stage are discussed in here. As described in Chapter 4, the first stage was a pair-wise round-robin tournament. Each pair-wise contest in the first stage consisted of 10 simulations in which agents with one strategy were introduced to a population of agents with another, and 10 simulations in which the first strategy dominated the population with the second invading. The mean frequency of a strategy over the last 2,500 simulation rounds was its score for that simulation. These scores were then averaged over 20 simulations, and this average recorded as the overall score for that strategy in that contest. Strategies were ranked according to average score across all pairwise contests.

MEMORY IN THE TOURNAMENT: DEFINITIONS AND DIFFICULTIES

Using submitted prose descriptions as well as the computer code submitted with or generated for each strategy, it is possible to divide the strategies entered to the tournament into a number of memory-use categories (Table 6.1). These categories by necessity neglect aspects of mental time travel (like theory of mind) that apply only to humans (and perhaps a few non-human animals) and instead concentrate on the use of memory by the computer agents. Thus it is possible to account for their 'understanding' of environmental changes and motivational states but must remain agnostic as to the emotional or representational content of these memories.

Category 0 indicates that the strategy made no use of *myHistory*. Ignoring their age, past moves, and the results of those moves, these strategies relied on a range of other methods (in one not quite serious entry, the digits of π) to determine their next move. Categories 1 and 2 describe those strategies that were relatively inflexible, deciding on future moves based on the agent's age or previous moves. This type of strategy partially used its memory, gleaning from it aspects of the agent's history, but neglecting the actual outcomes, in terms of payoff or environmental information that could be used to plan for future environmental changes. Category 3 describes strategies that pay close attention to their histories and use the information in *myHistory* to ascertain when a drastic environmental change has occurred. They can then adjust their behaviour accordingly. Finally category 4 strategies use all the information encoded in *myHistory*. Similar to category 3, they are capable of detecting environmental change but they can also use past information to predict the likelihood of future environmental changes (i.e. the exact value of p_c, or other error rates) and to act accordingly. Another important feature of category 4 strategies is their ability to discount information based on the time since acquisition of the information *and* the likelihood of environmental change occurring in the intervening time. In order to do this, they typically catalogue past instances in which a particular behaviour was used and keep track of instances in which that behaviour did not return the expected payoff – perhaps the closest thing to episodic memory the tournament agents achieved.

Table 6.1. Loose memory categories in the tournament strategies.

	Memory type	Example	Example strategies
0	Minimal use of declarative memory	e.g. I know one act, that's what I'll do	exploitOneInnovation, genderedStrategy, piRounds
1	Used memory as a guide for their next action in terms of agent's age only.	e.g. If I am 7 rounds old, do this	aHandfulOfSkill, innovateAndObserve, observeNoThanks, keepUp
2	Used memory as a guide for their next action in terms of last action only.	e.g. if I did this in the last round, do that in the next	anyRandGambit,
3	Used memory to generate an estimate of temporally local environmental conditions.	e.g. my payoff dropped in the last round, so I have undergone environmental change, better do this	copyIfBetter, balancedCopyWhenPayoffsDecrease, infantJuvinileMature
4	Used memory to estimate environmental parameters and use these to predict the probability of certain environmental changes in the future or discounting (see below)	e.g. I have estimated that there is a 95% chance of an environmental change in the next round, better do this next	W00t, discountMachine, prospero, whenTheGoingGetsThoughGetScrounging

This categorisation allows examination of the complexity of memory use and the link between the past and future aspects of mental time travel. Dudai and Carruthers (2005) suggest that there is a strong link, in the human mind at least, between memories of the past and prediction of the future. It is common sense to assume that prediction of the future without access to information about the past is little more than guessing, but equally it is possible that using memory in the very short term, noticing sudden changes, for example, without using that information to generate predictions about the future is almost equally fruitless. It is therefore possible that the selective advantage of episodic memory lies in its application to future events (Suddendorf and Corballis 2007, Tulving 1983). If this were the case, we would expect to see that the average scores of strategies in the pairwise contest of the tournament were similar for strategies using memory alone (category 3) and higher for those using both memory and future planning (category 4).

RESULTS

Memory categories were analysed in terms of median score using a Kruskal-Wallis test. The memory categories (0,1,2,3,4) were significantly different from each other ($p<0.001$) at the 95% confidence level. Category 4, incorporating both use of memory, discounting and prediction of future environmental changes, had the highest median score (Figure 6.1) and was significantly higher than categories 0, 1, 2 and 3. Both the eventual winner of the tournament, *discountmachine*, and the second place strategy, *intergeneration*, were in category 4, and of the top twenty strategies in the first round of the tournament, 10 were from category 4 and 4 were from category 3.

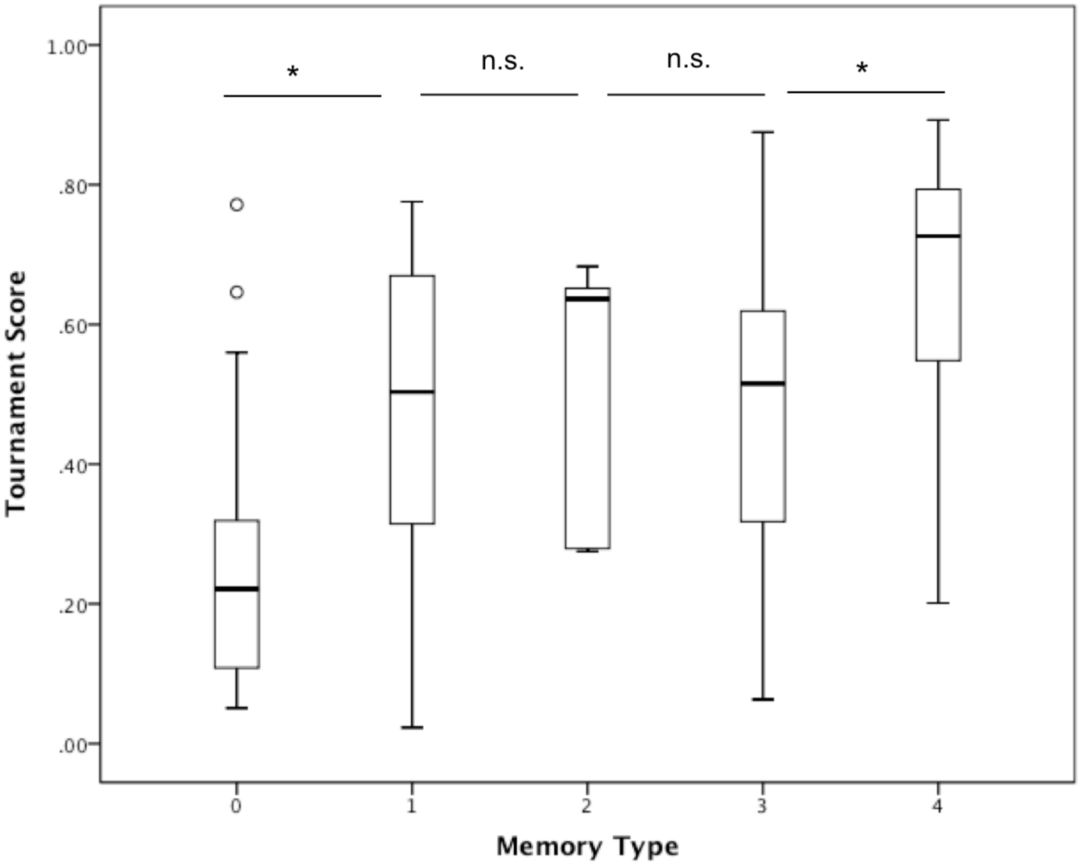

Figure 6.1. Plot shows memory category (0,1,2,3,4) against tournament score for all 104 strategies in stage 1 of the tournament. Median score shown (± interquartile range and maximum and minimum values). *$p < 0.05$, n.s implies non-significance.

The original analysis of the tournament strategies also stressed the importance of timing learning moves, whether social or asocial (Figure 4.8e). The analysis showed that the ability to time learning moves to coincide with environmental changes was crucial to success in the tournament. Effective timing of learning combines elements of both category 3 and 4 memory use. The positive relationship between the number of learning moves that were social, and a good strategy's success in the tournament, coupled with a negative relationship between social learning and success in the poorer performing strategies, implies that social learning is adaptive only when used well. This suggests that natural selection could have selected for more efficient use of social learning and the analysis here suggests that investment in mental time travel may be one means of increasing this efficiency.

DISCUSSION

It is of course difficult to discuss aspects of the strategies submitted to the tournament in isolation since, as the original analysis of the tournament results showed, there were a number of factors that contributed to the success or otherwise of each strategy (Chapter 4). The most important factors that emerged from that analysis were the proportion of learning moves that were social, and the timing of those learning moves (Chapter 4). It is easy however to see that there might be a significant link between the ability to time social learning moves correctly and the strategy's use of mental time travel.

The tournament winner, *discountmachine*, was a complex (category 4) strategy in terms of memory use. The most important and robust features of the strategy were (1) its overwhelming propensity to engage in social learning at the expense of individual learning (the strategy could only INNOVATE in one circumstance, when it was in the founding generation of a new simulation), (2) the timing of its social learning moves, which coincided optimally with environmental changes, and (3) its ability to discount information based on the age of the information and an estimate of the rate of environmental change.

There were a number of memory-related reasons for the success of *discountmachine*. The strategy adopted a forward-looking approach to making decisions in a way not seen in any of the other strategies. It chose between EXPLOIT and OBSERVE by using the closed form of a geometric series to compare the expected payoff gains from each move. It considered the gains expected from either exploiting the best act currently known until death or a change in payoff, or observing once and then exploiting the expected observed payoff, again until death or a change in payoff. The strategy chose to play OBSERVE if

$$w_{max}\left(\frac{1}{1-d}\right) < O_{est}\left(\frac{d}{1-d}\right), \tag{6.1}$$

where w_{max} is the maximum of the expected payoffs currently available in the agent's repertoire, O_{est} is an estimate of the expected payoff of an observed act calculated simply as the mean of all the observed payoffs in the agent's history, and d is a 'discounting' factor given by the product of the probability the agent will be alive in the next iteration and the agent's current estimate of p_c,

$$d = (1 - p_{est})(1 - p_{death}) \,. \tag{6.2}$$

Both *discountmachine* and the strategy that came in second overall in the tournament, *intergeneration*, used the same formula to discount information based on its age, specified in Equation 4.1

The formula discounts the value of information towards the estimated mean for all behaviours as the time since acquisition increases. The success of the strategies using this kind of flexible discounting suggests the possibility that natural selection could have shaped memory in a similar way. The strategies suggest that the ability to discount information based on experience of the past and prediction of the future is an important part of survival in changeable environments. The winning and runner-up strategies contrast with a number of less successful strategies in their ability to discount the value of information. Less successful strategies, although also capable of discounting, did so in a fixed and unresponsive way. For example, both *dynamicaspirationlevel* (3rd in round 1) and *spynwork* (34th in round 1) discounted information according to different rules. *spynwork* behaved in a rational way, exploiting only its best act but only considering acts updated in the last 25 rounds. This amounts to generating a fixed estimate of the rate of environmental change to be $p_c = 0.04$, or one change every 25 rounds. *dynamicaspirationlevel* was similar but decayed the value of all behavior by a set amount each round. Again this made an assumption about the rate of environmental change without specific reference to what the agents actually knew about the simulation environment and the probability of change. The kind of discounting that these strategies engaged in is arguably similar to the kind of discounting observed in stickleback fish. In the face of conflicting social information, these fish were shown to value their asocial information less as time passed since they collected the information (Van Bergen *et al.* 2004). It may be reasonable to assume that the costly calculations involved in constantly updating predictions about the world may not be worthwhile in all circumstances, and that in the absence of extreme variability in environmental conditions, natural selection may fashion some useful ‘rules of thumb’ about information discounting.

An analysis of the tournament strategies from the perspective of their memory use may go some way towards explaining why humans are particularly good at social learning – humans, perhaps alone, are capable of the kind of complex mental time travel required to maximize the benefits of social learning and ensure that any investment in social learning is strategic and low-risk. For instance, *discountmachine* computed whether investment in further learning would likely reap greater dividends in the future than relying on current behavior given its estimate of environmental change and the age of the information. It is possible that only humans are capable of this kind of calculation and that deployment of this kind of reasoning greatly enhances the efficiency of learning. Results from the tournament suggest strategic use of memory must be combined with strategic forgetting or discounting in order for a strategy to be successful.

SECTION 3:

CULTURAL NICHE CONSTRUCTION

SECTION 3, CHAPTER 7

RUNAWAY CULTURAL NICHE CONSTRUCTION

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INTRODUCTION

In recent years, there has been increasing recognition of the significance of niche construction, the capacity of organisms to modify natural selection in their environment and thereby act as co-directors of their own, and other species', evolution (Lewontin 1983; Odling-Smee *et al.* 2003). Examples of niche construction include animals manufacturing nests, burrows and webs and plants modifying nutrient cycles. The defining characteristic of niche construction is not modification of the environment *per se*, but rather an organism-induced change in the selective environment; hence the term includes migration, dispersal and habitat selection, where organisms relocate in space and experience new conditions, as well as traits that have a negative effect on the constructor's fitness, such as habitat degradation (Odling-Smee *et al.* 2003).

Genetic and ecological models have demonstrated that niche construction can affect evolutionary outcomes, even without culture (Laland *et al.* 1996, 1999; Odling-Smee *et al.* 2003; Day *et al.* 2003; Silver and DiPaolo 2006; Kylafis and Loreau 2008). For instance, niche construction can fix genes that would otherwise be deleterious (Laland *et al.* 1996, 1999), allow the persistence of organisms in inhospitable environmental conditions that would otherwise lead to their extinction (Kylafis and Loreau 2008), and be favoured even when costly because of the benefits that will accrue to distant descendants (Lehmann 2008). However, mathematical models reveal that niche construction due to cultural processes can be even more potent than gene-based niche construction, and demonstrate that cultural niche construction can modify selection on human genes with resulting effects on evolutionary outcomes (Laland *et al.* 2001; Odling-Smee *et al.* 2003; Boni and Feldman 2005; Borenstein *et al.* 2006; Laland 2008). Indeed, human niche construction is informed by a uniquely potent and cumulative cultural knowledge base (Odling-Smee *et al.* 2003; Smith 2007).

It is highly likely that human cultural niche construction has co-directed human evolution (Laland *et al.* 2000, 2001; Borenstein *et al.* 2006; Laland & Brown 2006; Laland *et al.* 2007, 2010; Richerson *et al.* 2010). In the last 100*kyr* humans have spread from East Africa around the globe, experienced an ice age, begun to exploit agriculture, witnessed rapid increases in densities, domesticated hundreds of species of plants and animals, and, by keeping animals, experienced a new proximity to animal pathogens (Laland *et al.* 2007; Smith 2007). Each of these events represents a major transformation in human selection pressures, and all (except the ice age) have been self-imposed. Humans have modified selection, for instance, by dispersing into new environments with different climatic regimes, devising agricultural practices or domesticating livestock. Niche-construction theory leads to the expectation that gene-culture co-evolution has been a general feature of human evolution (Laland *et al.* 2010).

This perspective is reinforced by analyses of data from the human genome, which have revealed numerous genes that have experienced recent positive selection, many of which exhibit functions that imply they are responses to human cultural practices (Voight *et al.* 2006; Wang *et al.* 2006; Sabeti *et al.* 2006, 2007; Nielsen *et al.* 2007; Williamson *et al.* 2007; Laland *et al.* 2010). For instance, several lines of evidence demonstrate that dairy farming created the selective environment that favored the spread of alleles for adult lactose tolerance (Durham 1991; Holden & Mace 1997; Burger *et al.* 2007; Tishkoff *et al.* 2007). Similarly, Perry *et al.* (2007) found that copy number of the salivary amylase gene (*AMY1*) is positively correlated with salivary amylase protein level and that individuals from populations with highstarch diets have, on average, more *AMY1* copies than those with traditionally low-starch diets. Higher *AMY1* copy numbers and protein levels are thought to improve the digestion of starchy foods, consumed at elevated levels by agricultural populations, and may buffer against the fitness-reducing effects of intestinal disease. The transition to novel food sources with the advent of agriculture would appear to have been a major source of selection on human genes, and several genes related to the metabolism of protein, carbohydrates, lipids and phosphates show signals of recent selection (Richards *et al.* 2003; Voight *et al.* 2006; Wang *et al.* 2006; Williamson *et al*. 2007). In turn, agricultural and the domestication of animals is known to have facilitated the spread of crowd diseases and zoonoses, generating selection for human genes that confer resistance to these diseases in regions where they are prevalent (Saunders *et al.* 2002; Thompson *et al.* 2004; Voight *et al.* 2006; Wang *et al.* 2006; Sabeti *et al.* 2006; Nielsen *et al.* 2007). Cultural niche construction could also have selected for enhanced cognitive capabilities (Richerson *et al.* 2010), and many of the alleles subject to recent selection are known to be expressed in the brain (Voight *et al.* 2006; Wang *et al.* 2006; Laland *et al.* 2010).

Estimates for the number of human genes subject to recent rapid evolution range from a few hundred to two thousand: Williamson *et al*. (2007) conclude that as much as 10% of the human genome may be affected by linkage to targets of positive selection. While, in the vast majority of cases, it is not known what phenotype was the target of the inferred selection, nor which environmental conditions favoured such phenotypes, human cultural practices remain primary candidates, and geneticists are increasingly considering culture as a source of selection on humans (Hawks *et al.* 2007; Varki *et al.* 2008; Laland *et al.* 2010).

One of the best-researched cases is the haemoglobin *S* allele (*HbS*), famous as a textbook case of heterozygote advantage, since it provides protection against malaria in the heterozygote form. Durham (1991) studied populations of Kwa-speaking agriculturalists from West Africa, who cut clearings in forests to grow crops, often yams. The removal of trees had the effect of inadvertently increasing the amount of standing water when it rained, which provided better breeding grounds for malaria-carrying mosquitoes, which intensified selection on *HbS*. The fact that adjacent populations whose agricultural practices are different do not show the same increase in allele frequency supports the conclusion that cultural practices can drive genetic evolution. Moreover, this example illustrates how it may be necessary for models to take account of the frequency of resources modified through human niche construction (in this case, the amount of standing water) if they are to capture co-evolutionary dynamics accurately.

Human agricultural practices are tied to specific spatial locations, and the selective feedback on human genes resulting from such practices, whether related to diet, disease resistance or morphology, is likely to co-vary in space with the incidence of the practice. Accordingly, there is a need for spatially explicit models with which to better understand how some human cultural processes have interacted with human genes during recent human evolution, whilst simultaneously tracking the frequency of relevant resources. While there has been extensive modelling of human gene-culture coevolution (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Kumm *et al.* 1994; Aoki & Feldman 1991, 1997; Richerson and Boyd 2005; Mesoudi & Laland 2007; Enquist *et al.* 2007; Laland *et al.* 2010; Richerson *et al.* 2010), thus far spatial effects have been comparatively neglected. However, the introduction of spatial structure and stochasticity in finite populations is known to affect evolutionary outcomes when compared with non-spatial models (Durrett & Levin 1994a,b; Krakauer & Pagel 1995). Moreover, spatially explicit models of gene-based niche construction have revealed that niche-constructing traits can drive themselves to fixation by creating statistical associations with the recipient traits they favour (Silver & DiPaolo 2006). Niche-constructing alleles expressed in the modification of local resources transform environmental conditions to favour some genotypes, and provided mating and dispersal is local, the niche-constructing alleles can hitchhike across a landscape to fixation.

Here spatially explicit gene-culture co-evolutionary models are developed to explore the interaction between local cultural niche construction and genetic evolution. The aim was to explore whether interactions between cultural traits and alleles mediated by niche construction can create the conditions under which runaway selection can lead to evolutionary outcomes that can overcome external natural selection. The models therefore investigate whether, and under what circumstances, cultural niche-constructing practices can 'run away' with genetic variation, and to what extent this dynamic is affected by (*i*) cultural transmission biases operating against the niche-constructing trait, (*ii*) the cost of cultural niche construction, modelled as a viability deficit to the cultural practice, and (*iii*) a viability cost to the genotype favoured by cultural niche construction. The models also investigate (i*v*) whether genetic variation enhancing the capability for cultural niche construction can be favoured by this runaway dynamic. The analysis concentrates on three questions:

1. Can a culturally transmitted niche-constructing practice become universal, even when costly, through statistical association with a genetic trait it favours?

2. Can cultural niche construction generate selection for costly genetic traits that confer improved ability to cope with, or exploit the products of, said niche

construction (for example, genes expressed in disease resistance, or an expensive digestive protein)?

3. Can cultural niche construction favour the secondary hitchhiking of costly capabilities at other loci, which confer more powerful niche-constructing abilities on the bearer (e.g. bigger brains)?

METHODS

The model presented here marries the spatially explicit individual-based methods of Silver and Di Paolo (2006) with the gene-culture co-evolutionary analysis of Laland *et al.* (2001). It therefore draws on simpler, well-understood systems to provide a foundation for exploring these complex co-evolutionary processes. The model has a finite population of diploid individuals. It focuses initially on a single diallelic resource-dependent locus, **A**, with alleles *A* and *a*, and a single two-state cultural niche-constructing practice, **E**, with variants *E* and *e* (see Table 7.1), but adds a further genetic locus, **B**, for later analyses.

Table 7.1: Probabilities of vertical cultural transmission of *E* and *e* given parental traits

Parental traits	Probability of *E* offspring	Probability of *e* offspring
$E \times E$	c_3	$1\text{-}c_3$
$E \times e$	c_2	$1\text{-}c_2$
$e \times E$	c_1	$1\text{-}c_1$
$e \times e$	c_0	$1\text{-}c_0$

Following Silver and Di Paolo (2006), individuals are arranged in an $n \times n$ square lattice with wrap-around (toroidal) boundaries. Each lattice point (i, j) is occupied by a single individual with phenogenotype $\{\mathbf{A}_{ij},\mathbf{E}_{ij}\}$ and has an associated, local environmental resource frequency $\{R_{ij}\}$. Each individual has eight nearest neighbours (its Moore neighbourhood). Alleles make a contribution to fitness that is in part a function of the local resource frequency. Resource frequencies are subject to change as a result of (*i*) the niche-constructing activities of individuals in the population, and (*ii*) independent processes of depletion and renewal. An individual's capacity for niche construction depends on the cultural practice deployed, with *E* individuals exhibiting niche construction, and *e* individuals exhibiting no niche construction. As in Laland *et al.* (2001), if $p_{t-1}(E)$ is the frequency of the trait *E* in the population at time *t*-1, the amount of the resource, *R* at time *t* is given by

$$R_t = \lambda_1 R_{t-1} + \lambda_2 p_{t-1}(E) + \lambda_3 . \tag{7.1}$$

Here, λ_1 is the coefficient of independent depletion of the resource; λ_2 is the coefficient of positive niche construction, corresponding to niche-constructing activity that increases *R* (assuming only positive niche-construction); λ_3 is a coefficient of independent renewal of the resource. Following Silver and Di Paolo (2006), a scalar version of this equation is applied at each lattice point. At any particular lattice point, *p(E)* takes one of the values {0, 1} corresponding to the two possible cultural states, respectively {*e*, *E*}. Local resource frequency is thus a function of independent processes of depletion and renewal, and of the cumulative effect of local niche-construction activity over preceding generations. Following Laland *et al.* (2001), $0 < \lambda_1, \lambda_2, \lambda_3$ and $\lambda_1 + \lambda_2 + \lambda_3 \leq 1$, such that the local resource frequency, R_{ij}, can take any real value between 0, corresponding to complete absence of the resource, and 1, corresponding to resource saturation. Unless otherwise specified, these parameters were set to $\lambda_1 = 0.7$, $\lambda_2 = 0.2$, and $\lambda_3 = 0.1$ in the simulations reported here. These values mean the resource depletes in the absence of niche construction to an equilibrium of $\frac{\lambda_3}{(1-\lambda_1)}=1/3$. For example, in the case of the aforementioned Kwa, the amount of standing water is a function of independent renewal (i.e. rainfall), independent depletion (e.g. evaporation, runoff, absorption) and niche-constructing activities over multiple generations (e.g. planting crops, which reduces absorption and thereby increases standing water). All variables and coefficients are dimensionless.

Fitnesses were allocated to combinations of genotype and cultural practice, henceforth ‘phenogenotypes’, as specified in Tables 7.2-7.4, which are tailored to addressing questions 1-3 above. Genotype fitness depended both on resource frequency and on selection from an external source. In all models the baseline fitness of the three genotypes are as follows:

$$\begin{aligned} f_{AA} &= \eta_1 + \varepsilon R, \\ f_{Aa} &= 1 + \varepsilon\sqrt{R(1-R)}, \\ f_{aa} &= \eta_2 + \varepsilon(1-R), \end{aligned} \tag{7.2}$$

where $R = R_{ij}$, the resource frequency at the individual’s lattice point. The first terms in each of these fitness relations correspond to fixed-fitness components, representing the effect of external selection operating at **A**. The second terms refer to the resource frequency-dependent components of selection, and it is these that are affected by niche construction. The coefficient of proportionality ε determines the strength (relative to external selection), and direction of resource-based frequency-dependent selection, with positive ε indicating that increased environmental resource levels will favour the *A* allele. In all simulations reported in this chapter $\varepsilon = 0.3$. A summary of all parameters used is given in Table 7.5.

Individuals mate with a randomly chosen neighbour (Moore neighbourhood), and offspring inherit their parents' genotypes in Mendelian proportions. Here both vertical and oblique transmission of cultural traits is considered. Vertical transmission occurs according to the parameters specified in Table 7.1. Offspring (viability) fitness is determined with reference to the resource level at one (randomly selected) parent's location, under the assumption that newborn offspring develop in the same location as one of their parents. The probability of an offspring surviving is proportional to its fitness related to the minimum and maximum values of equation 7.2 given the selection coefficients in a given simulation and the limits of R (0,1). Offspring surviving to the dispersal stage are placed in a cell chosen at random from the 8 cells in the neighbourhood of the parent with which the newborn develops, plus that parent's own cell, replacing the original occupant. These individuals are then considered adult and capable of reproduction. In this way fitter offspring may spread out to colonise neighbouring cells, while an effective carrying capacity equal to the total population size is maintained. Following Silver and Di Paolo (2006), a generation is defined as n^2 consecutive random matings, so that there will be significant overlap between one generation and the next.

Here questions 1-3 are considered in turn, in each case a series of simulations were run to explore the behaviour of the system, using the parameters and fitness equations described in tables 7.2-7.4, respectively. For each set of parameter values the starting frequencies of A and E were varied independently from 0.1 to 0.9 in 0.1 increments, giving 81 different starting conditions, and 10 simulations were run at each one. Spatial models ran in a 60×60 toroidal grid, and non-spatial models had the same population size of 3600 individuals. Alleles were distributed randomly and independently of each other at the start of each simulation, such that genotype frequencies at the start of the simulation averaged Hardy-Weinberg proportions, and cultural traits were randomly distributed across individuals irrespective of genotype. Lattice points were assigned uniform randomly distributed starting resource values (R) between 0 and 1. For each analysis there were non-spatial controls in which the 'neighbourhoods' for mating and dispersal comprised the entire lattice so that individuals and resource locations were picked at random from the general population. All simulations ran until A (question 1), E (question 2) or A and E (question 3) became either fixed or extinct, or simulations reached 1,000 generations.

1. Can a cultural niche-constructing practice drive itself to fixation, even when costly, through statistical association with a genetic trait it favours?

A costly niche-constructing practice E (selection coefficient $\alpha<1$) is considered, which increases the amount of resource R in the environment and generates selection favouring allele A. Phenogenotype fitnesses are specified in Table 7.2. Here the analysis explores how a transmission bias for and against the cultural practice E (i.e. variation in $c=c_1=c_2=\{0.45, 0.5, 0.55\}$, $c_0=0$, $c_3=1$), and selection against E (α), affect the dynamics.

Table 7.2: Pheno-genotype fitness functions to explore the evolution of costly cultural niche construction (*a* is the selection coefficient operating on the cultural practice *E*).

	E	***e***
AA	$w_{11}=\alpha+\varepsilon R$	$w_{12}=1+\varepsilon R$
Aa	$w_{21}=\alpha+\varepsilon\sqrt{R(1-R)}$	$w_{22}=1+\varepsilon\sqrt{R(1-R)}$
aa	$w_{31}=\alpha+\varepsilon(1\text{-}R)$	$w_{32}=1+\varepsilon(1\text{-}R)$

2. Can cultural niche construction generate selection for costly genetic traits?

A costly genetic trait AA (selection coefficient $h\leq1$), that is favoured by the niche-constructing practice E (selection coefficient $\alpha=1$) is considered. Here, the increase in resource due to niche-construction depends on the frequency of both *A* and *E*. The modified version of Equation 7.1 used to update the resource level, and the relevant phenogenotype fitness functions, are specified in Table 7.3. A transmission bias for and against the cultural practice *E* (*c*) and selection against the *AA* genotype (*h*) affect the dynamics are also explored.

Table 7.3: Phenogenotype fitness functions to explore the evolution of a costly capability to exploit cultural niche construction.

Genotype	Fitness
AA	$w_{11}=h+\varepsilon R$
Aa	$w_{21}=1+\varepsilon\sqrt{R(1-R)}$
aa	$w_{31}=1+\varepsilon(1-R)$

where $R_t = \lambda_1 R_{t-1} + \lambda_2 u + \lambda_3$ and *u* is the frequency of *AE*.

3. Can cultural niche construction favour the secondary hitchhiking of costly capabilities at other loci, expressed in more potent niche construction?

For this question a second genetic locus, **B**, with alleles *B* and *b*, where allele *B* enhances the rate at which niche constructors produce resource *R* is introduced. Homozygous *BB* individuals have selection coefficient β_1, those with *bb* have coefficient β_2, and heterozygotes (*Bb*) have $(\beta_1+\beta_2)/2$. In individuals with the cultural trait *E* (selection coefficient $\alpha=1$), *BB* enhances niche construction by proportion 1+*f*, and *Bb* by proportion 1+*f*/2 (although the condition $0 \leq R \leq 1$ was still applied). The modified version of Equation 7.1 was used to update the resource level, and the relevant phenogenotype fitness functions are specified in Table 7.4. The effects of a transmission bias for and against the cultural practice *E* (*c*), and selection against the *B* allele ($\beta_1<1$, $\beta_2=1$), on the evolutionary dynamics are considered.

Table 7.4: Can niche construction favour the hitchhiking of costly capabilities at other loci?

	BB **(β_1)**	***Bb*** **((β_1+β_2)/2)**	***bb*** **(β_2=1)**
AA **(*h*=0.999)**	$w_{11}=\beta_1+\varepsilon R$	$w_{12}=(\beta_1+\beta_2)/2)+ \varepsilon R$	$w_{13}=1+\varepsilon R$
Aa **(1)**	$w_{21}=\beta_1+\varepsilon \sqrt{R(1-R)}$	$w_{22}=(\beta_1+\beta_2)/2)+ \varepsilon \sqrt{R(1-R)}$	$w_{23}=1+\varepsilon \sqrt{R(1-R)}$
aa **(1)**	$w_{31}=\beta_1+\varepsilon (1-R)$	$w_{32}=(\beta_1+\beta_2)/2)+ \varepsilon (1-R)$	$w_{33}=1+\varepsilon (1-R)$

where $R_t = \lambda_1 R_{t+1} + \lambda_2 (z_1(1+f) + z_2(1+\frac{f}{2}) + z_3) + \lambda_3$, where z_1,z_3 are the frequencies of *BBE, BbE* and *bbE* individuals, respectively.

Table 7.5: Summary of parameters

Parameter	Explanation
E,e	Alternative niche-constructing cultural practices
A,a	Alleles at **A** locus
B,b	Alleles at **B** locus
R	Resource frequency
λ_1	Independent resource depletion
λ_2	Positive niche construction
λ_3	Independent resource renewal
p(*E*)	Frequency of *E* cultural practice
γ	Negative niche construction
ε	Strength and direction of resource frequency dependence
α	Selection coefficient acting on cultural practice
c_0	Probability *e* x *e* mating has *E* offspring
c_1	Probability *e* x *E* mating has *E* offspring
c_2	Probability *E* x *e* mating has *E* offspring
c_3	Probability *E* x *E* mating has *E* offspring
η_1	*AA* fitness
η_2	*aa* fitness
β_1	*BB* fitness
β_2	*bb* fitness
φ	Degree to which B potentiates niche construction
f	Probability of oblique transmission

RESULTS

Can a cultural niche-constructing practice drive itself to fixation, even when costly?

Across a broad range of conditions, cultural niche-constructing practices can generate selection for specific gene-based traits and hitchhike to elevated frequencies through the build up of statistical associations between practice and trait (Figures 7.1-7.3). This is most apparent where there is little or no fitness cost to the cultural practice (Figure 7.2, $\alpha \approx 1$), but is observed to a lesser degree even in the face of strong selection against E (e.g. a 5% disadvantage).

These dynamics occur because, initially by chance, clusters of niche constructors appear in specific regions of space, generating a local concentration of the resource R, which in turn generates selection that favours allele A. In the spatial model, individuals mate and reproduce locally. Under these circumstances, allele A becomes statistically associated with the niche constructing practice E, while allele a becomes associated with e. This means that the selection on A generated by niche construction inadvertently favours E through hitchhiking. Provided the clusters of niche constructors reach a critical threshold size they will typically increase until the trait is fixed. This assortative mating does not occur in the non-spatial model, preventing E from being disproportionately favoured by selection on A.

The cluster size effect represents a balance of several processes (Figure 7.1). The dynamics are similar to those observed in Silver and Di Paolo's genetic niche construction spatial model, but here there is the additional complication of cultural transmission biases. To understand the process, it is helpful to envisage two concentric circles, the smallest encompassing the cluster. Because the niche construction leads to non-random associations between the alleles and cultural traits, inside the inner circle are mainly AAE individuals, while outside the outer circle are mainly *aae* individuals. Separating the two is a boundary layer dominated by heterozygotes. Newly born *AAE* individuals disperse into the boundary layer from the inner circle, while newly born *aae* individuals enter the boundary layer from the outer region. Because the outer circle is larger than the inner circle, other matters being equal, this dispersal will tend to act to reduce cluster size. The magnitude of this force diminishes with cluster size, since the relative size of the two circles approaches 1 as the cluster increases. Opposing this process is the niche construction of those boundary layer individuals exhibiting the *E* cultural practice. This niche construction generates conditions that favour the *A* allele, which is disproportionately found in E individuals. Natural selection and cultural transmission also play a role, by affecting phenogenotype fitness (Figure 7.1). Provided the balance of these processes favours *E* over *e* within the boundary layer, then the clusters will increase in size.

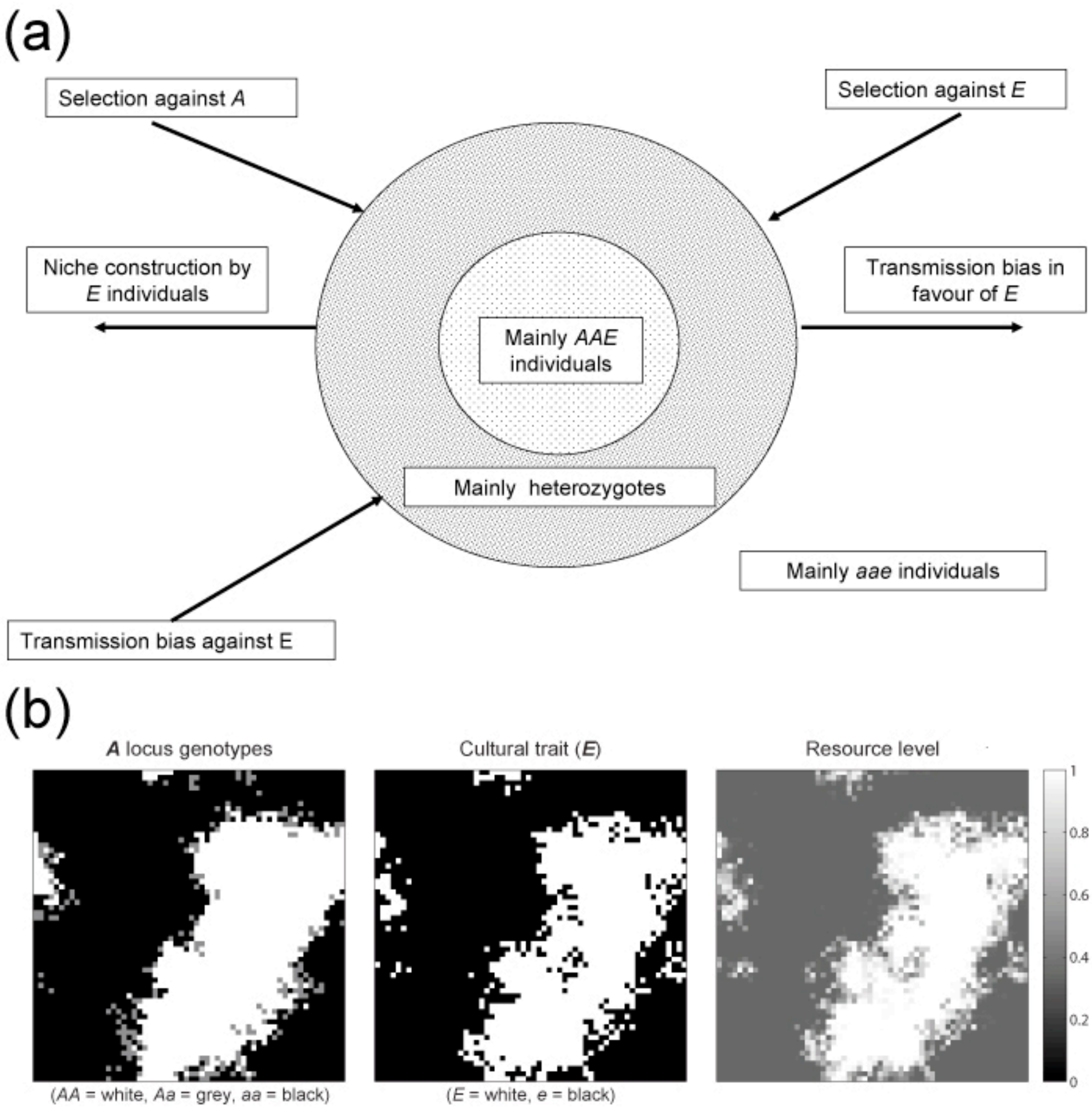

Figure 7.1: (a) Schematic diagram of evolutionary forces acting on spatial clusters of individuals carrying linked cultural niche construction traits and alleles favoured by niche construction. (b) Snapshot illustrating spatial clustering associations between *A*, *E*, and *R* during a simulation run of the evolution of a costly capability to take advantage of cultural niche construction (selection against *A* allele, η, = 0.95, no cultural transmission bias).

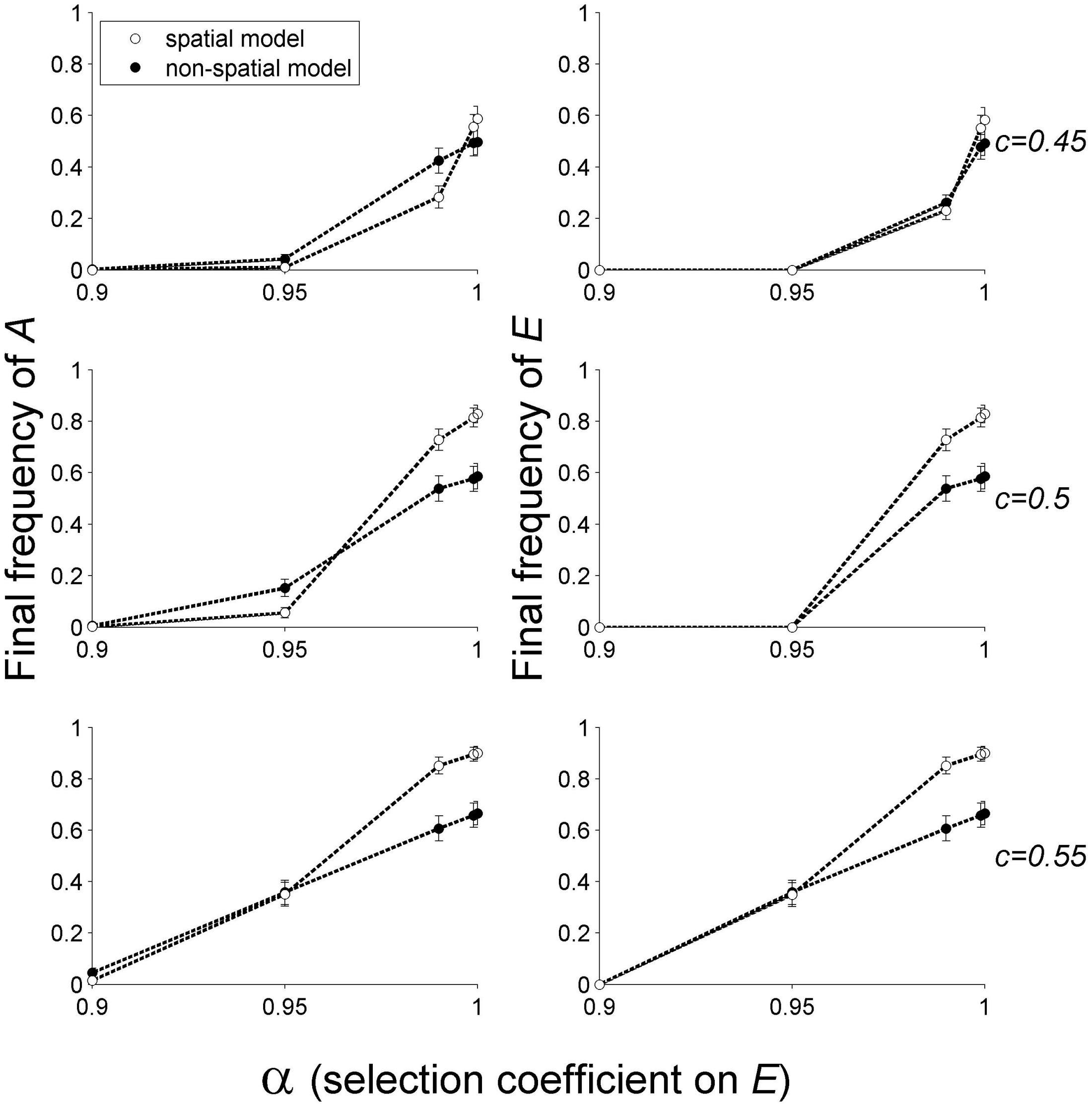

Figure 7.2: Evolution of costly cultural niche construction. Plots show frequency of allele *A* favoured by higher resource levels and cultural niche-constructing trait *E* at the end of simulations run with varying levels of selection against, and cultural transmission bias with respect to, *E* (α and c parameters respectively). Values are means over all starting conditions with respect to the initial frequencies of *A* and *E* and error bars show ±1 standard error. Open circles show results from simulations with local mating and dispersal, filled circles are from those with global interactions.

The model showed that cultural niche construction could overcome moderate and sometimes even strong counter selection, and evolve to high frequency, especially when there was no transmission bias or where a transmission bias favoured the practice (c>0.5) (Figure 7.2).

The similarity in outcome for both the *A* allele and the *E* cultural practice shows that strong associations built up between them under most conditions. Generally, in spatially structured populations *A* and *E* both reached higher frequencies on average than in fully mixed scenarios, except when counter-acting natural or cultural selection was very strong. This difference was driven largely by spatial structure, enabling both trait and practice to become established and increase from lower initial frequencies (Figure 7.3). When initial frequencies are very high or very low there are also differences between spatial and non-spatial model outcomes. These result from the possibility in spatial models that local gene frequencies can diverge significantly from population level frequencies. This can have a buffering effect that acts to preserve low-frequency alleles in pockets of local abundance in situations where a lack of spatial structure would lead to extirpation of the allele. The exception to this trend occurred when a cultural transmission bias (i.e. c<0.5) or extremely strong selection (i.e. a=0.9) acted against the *E* trait. In this case, the outcomes in mixed and structured populations were very similar. The effects described above break down when oblique transmission is very potent (i.e. the probability of learning from a non-parent is greater than 0.8), but that the effects persist with moderate or low levels of oblique transmission.

Can cultural niche construction generate selection for costly gene-based traits?

Here the results were very clear. Under almost all conditions a cultural niche construction trait could drive a genetic trait to fixation, in spite of a significant viability deficit to the trait. The only exception occurred when a cultural transmission bias against the niche-constructing practice and a very strong viability deficit to the trait were both acting together. The aforementioned dynamic, resulting from the association of genetic trait and cultural practice, is sufficiently strong to overcome strong counter selection (e.g. >5% disadvantage). Even more striking is the observation that a modest cultural transmission bias favouring the practice can generate selection that takes extremely low fitness traits (e.g. >10% disadvantage) to fixation. That this is not dependent on spatially mediated hitchhiking is illustrated by the observation of the same process operating in non-spatial populations, and is consistent with earlier analyses of the impact of cultural niche construction (Laland *et al.* 2001). The niche construction allows allele *A* to reach high frequencies when counter-selection was moderate to weak, and persist at non-negligible frequencies even in the face of potent counter-selection (Figure 7.4). Only a moderate cultural transmission bias (i.e. $c>0.5$) is required to strongly favour the niche constructing practice so that both allele and cultural practice nearly always evolve to fixation even when initially quite rare (Figure 7.5). Again, spatial structure facilitates the spread of these traits to higher frequencies than in mixed populations. The values chosen for $\lambda_1, \lambda_2, \lambda_3$, and ε mean that the fitness functions defined in Equation 7.2 produce an asymmetry with respect to that portion of fitness that relates to the level of *R* that favours the *A* allele (in the long-term presence of *E*, $R \rightarrow 1$, so the second term of the fitness function for *AA* evaluates to ε while for *aa* in the long-term presence of *e* this evaluates to $2\varepsilon/3$). Not surprisingly, altering the dynamics of the niche constructing ecology via these parameters can alter the model outcomes such that the coevolution of *A* and *E* no longer occurs.

In terms of starting frequencies, the switch between those resulting in extinction of the trait and those resulting in fixation occurred over much smaller change in starting conditions than the previous analysis. Under some conditions, particularly when cultural transmission biases favour *E*, a change in the starting frequencies of either allele by 0.1 can shift the outcome from a high probability of extinction to a near-certainty of fixation, suggesting that factors such as drift, bottlenecks or founder effects could play a significant role in shifting populations from one state to another.

Can cultural niche construction favour the secondary hitchhiking of costly capabilities at other loci, expressed in more potent niche construction?

Here a similar analysis produced more ambiguous results, with *B* only hitchhiking to higher frequency under much more restricted conditions. Across the bulk of conditions under which *E* hitchhikes, *B* does not. While *A* and *E* both reach high frequencies, and exhibited a similarity of outcome that showed they were highly associated, there was no indication that *B* had formed any association with either *A* or *E*. To the contrary, its outcomes were independent of the practice and the alleles at the other locus, and appeared largely to be affected only by selection at **B**, even for large values of f (e.g. $f = 10$), and no matter the strength of cultural transmission bias, c. These results occur in spite of the fact that, even with $f = 1$, the effect of *B* on resource levels is dramatic.

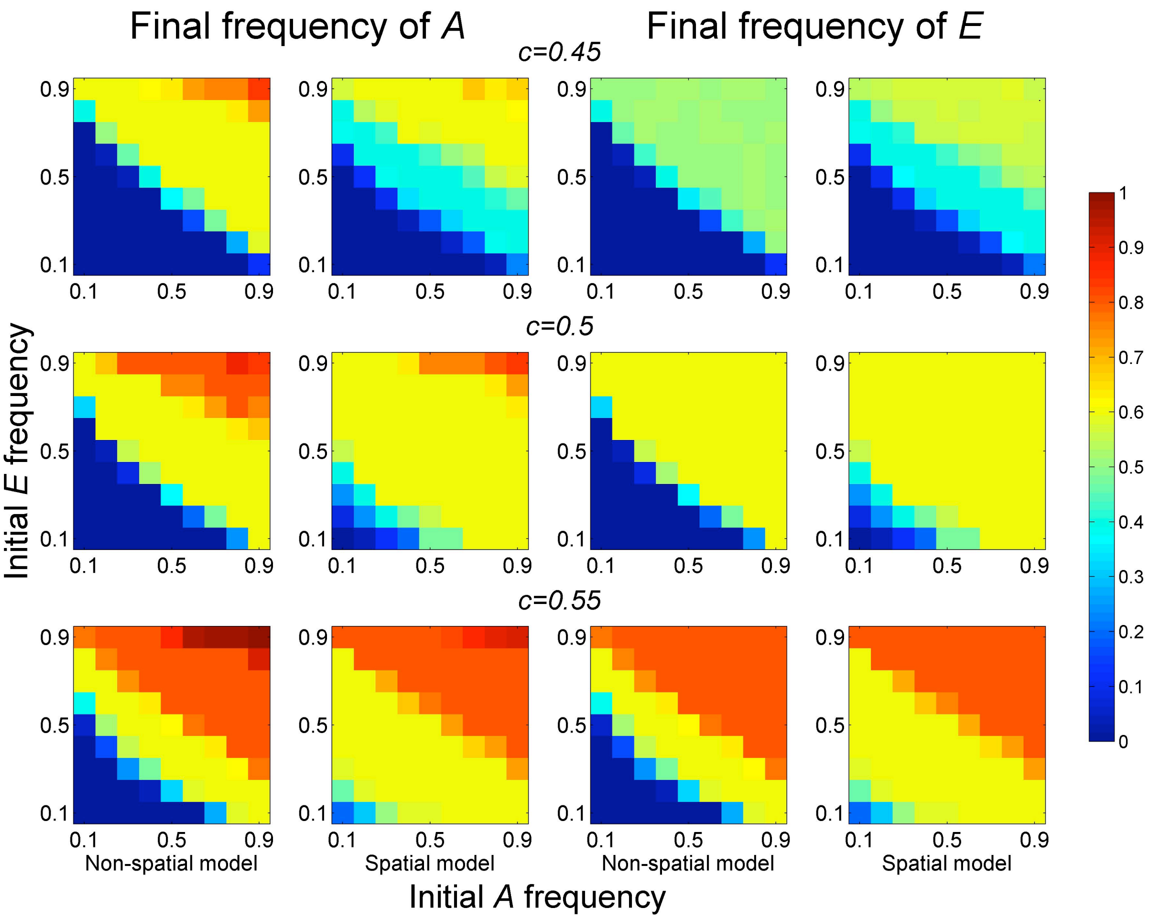

Figure 7.3: Effect of starting conditions on the evolution of costly cultural niche construction. Plots show end frequencies of *A* and *E* against their starting frequencies. Cell values are means over all levels of selection against *E* (α={0.9, 0.95, 0.99, 0.999, 1}).

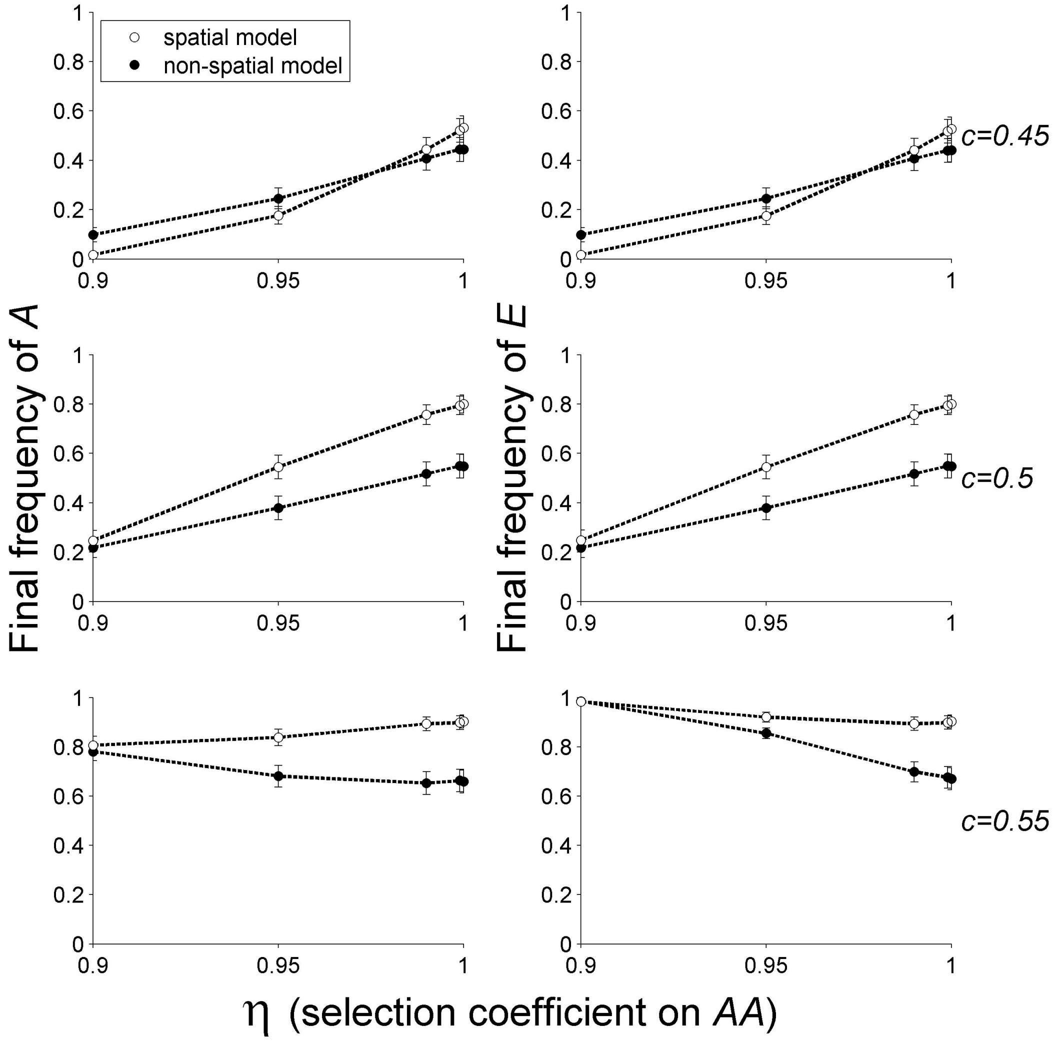

Figure 7.4: Evolution of a costly capability to take advantage of cultural niche construction. Plots show frequency of allele *A* favoured by higher resource levels and cultural niche-constructing trait *E* at the end of simulations run with varying levels of selection against the homozygote *AA* (η={0.9, 0.95, 0.99, 0.999, 1}), and cultural transmission bias with respect to *E* (*c*). Values are means over all starting conditions with respect to the initial frequencies of *A* and *E* and error bars show ±1 standard error. Open circles show results from simulations with local mating and dispersal, filled circles are from those with global interactions.

However, there is a restricted region of parameter space in which the secondary hitchhiking reliably occurs. It requires, perhaps counter-intuitively, a low coefficient of positive niche construction, λ_2. Figure 7.6 shows that *B*'s hitch-hiking lags behind the rapid and strong interaction between *A* and *E*; this is the characteristic pattern. There exists a window of low levels of positive niche construction, λ_2, under which secondary hitchhiking is apparent (Figure 7.7), with values of λ_2 too high or too low failing to lead to increased frequencies of *B*. When λ_2 is too high then the niche construction of individuals with *bb* genotype and the *E* practice is already potent, and the resource *R* reaches saturation before enough time has passed for an association of alleles *A* and *B* to build up. Once *A* and *E* become fixed, the opportunity for *B* to hitch-hike on them is lost. Conversely, when λ_2 is too low then the niche construction of *E* individuals with the *bb* genotype is too weak, so *A* and *E* simply never become established, and *B* cannot hitch-hike. Only when niche construction is within the window illustrated in Figure 7.7 are *A* and *E*'s spread to fixation sufficiently reliable and slow to allow linkages to build up between these and *B*. Once the association is established, typically in a confined spatial region, then the *AABBE* combination begins to expand. This effect was only observed in spatial models, and never in non-spatial ones. Spatial structure is absolutely essential for *B*'s spread because the requisite mutual reinforcement of the *A*, *E*, and *B* traits cannot happen if their effects are diluted and dispersed across a population.

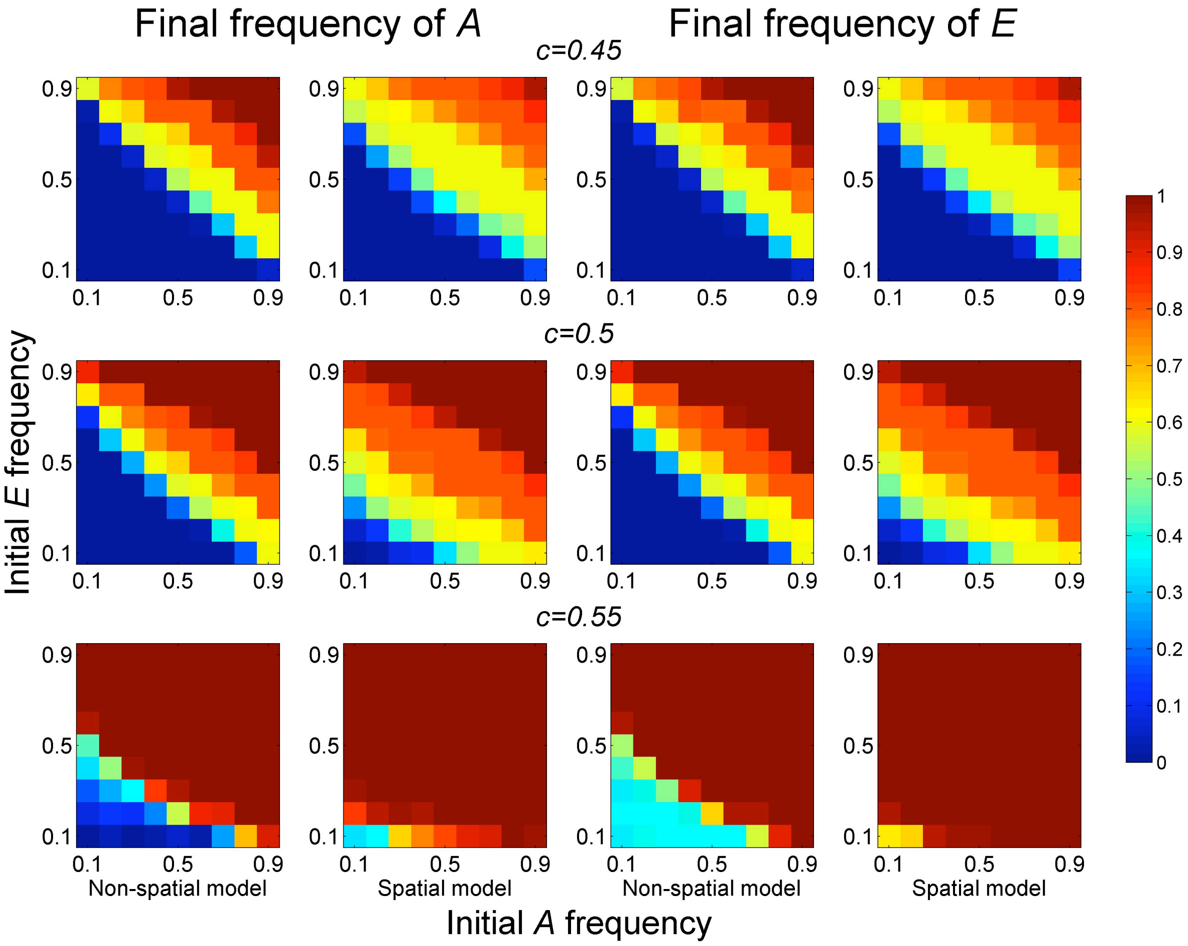

Figure 7.5: Effect of starting conditions on the evolution of a costly capability to take advantage of cultural niche construction. Plots show end frequencies of *A* and *E* against their starting frequencies. Cell values are means over all levels of selection against *A* (*h*).

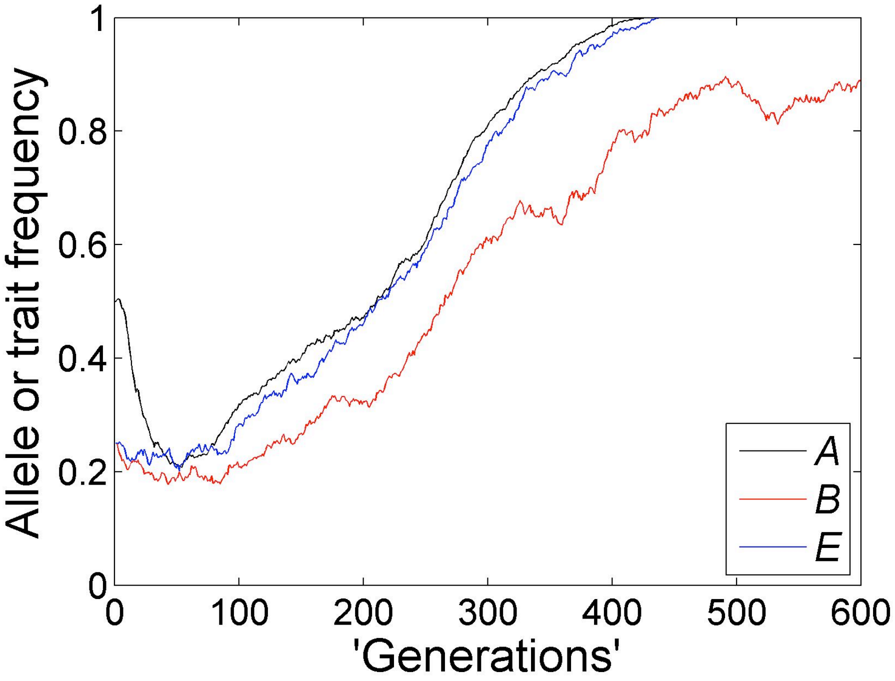

Figure 7.6: Time series of a single simulation run with $\lambda_2 = 0.06$, showing lagged hitch-hiking of *B* allele even when selection acts against *BB* ($\beta_1 = 0.99$). Note that after *A* and *E* fix (typically at this point the resource, *R*, will also be saturated), *B* can no longer hitch-hike and begins to show drift-like dynamics. Other parameters were cultural transmission bias, $c = 0.5$, selection on *AA*, $\eta = 0.999$, and selection on *bb*, $\beta_2 = 1$.

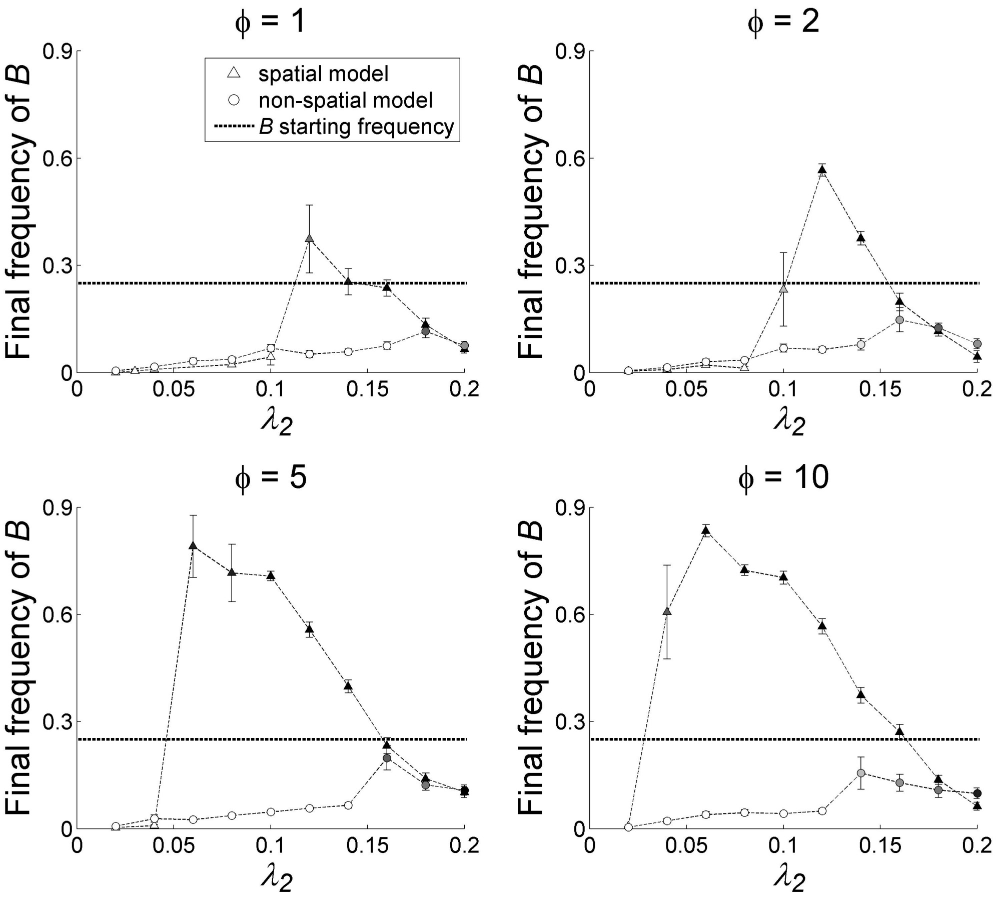

Figure 7.7: Effect of λ_2, the coefficient of positive niche construction, and *f*, the strength of *B*'s effect on niche construction, on the evolution of costly genes that potentiate niche-construction. Plots show frequency of allele *B* at the end of simulation runs, with each point representing the mean (± 1 standard error) of ten runs. Symbols are shaded according to the proportion of the ten runs in which *A* and *E* both fixed (white = no runs fixed, black = all runs fixed). All other parameters were fixed – cultural transmission bias, $c = 0.5$, selection on *AA*, $\eta = 0.999$, selection on *BB*, $\beta_1 = 0.99$, selection on *bb*, $\beta_2 = 1$. Initial frequencies of *E*, *A* and *B* were set at 0.25, 0.5 and 0.25 respectively. Note the high levels of *B* at intermediate values of λ_2 for spatial models only.

DISCUSSION

Here spatially explicit gene-culture coevolutionary models are presented to investigate how cultural processes could drive bouts of selection on human genes through modifying local resource distributions. The principle point to emerge from the analysis is that under a broad range of conditions cultural niche-constructing practices can generate selection for specific gene-based traits and hitchhike to fixation through the build up of statistical associations between practice and trait. This is most apparent where the fitness cost of the cultural practice is low but is observed to a lesser degree even in the face of very strong counter-selection. Cultural niche construction could overcome moderate and even strong counter selection and evolve to high frequency, especially when there was no transmission bias or where a transmission bias favoured the practice.

These dynamics are most pronounced in the spatially explicit models because niche construction and spatial structure lead the genetic trait and cultural practice to become statistically associated. This means that the selection on genes generated by niche construction inadvertently favours the cultural niche-constructing practice itself through hitchhiking. Provided the clusters of niche constructors reach a critical threshold size they will typically increase until the trait is fixed. The dynamics are similar to those observed in Silver & Di Paolo's genetic niche construction spatial model, but further complicated by cultural transmission biases. They are robust to moderate levels of oblique cultural transmission (here, learning from neighbours), although high levels of oblique transmission unsurprisingly make it harder to build up gene-culture correlations.

In essence, the dynamical process closely resembles that of runaway sexual selection. Geneticist R. A. Fisher (1930) proposed a positive feedback mechanism that could potentially explain the evolution of costly traits in animals that do not increase survival. Such traits were thought to be favoured because they increase the individual's attractiveness to the opposite sex. Subsequent analysis has established that if the preference reaches a sufficiently high frequency it can overcome a viability deficit to the trait and generate selection that will increase trait frequency. Since individuals with the trait mate assortatively with individuals with the preference, over time these characters become statistically associated, such that the selection on the trait leads to the preference hitchhiking to higher frequency (Lande 1981; Kirkpatrick 1982). The process is described as 'runaway' because over time it would facilitate the elaboration of both trait and preference.

Here the cultural niche construction practice (*E*) is analogous to the mating preference which, provided it is of sufficiently high frequency, could generate a selective environment that favours the otherwise costly allele *A*. There is strong support for the hypothesis that cultural niche construction can generate selection for costly gene-based traits. The cultural niche construction trait almost always drove the low viability genetic trait to fixation, with the only exception being where both natural selection and a transmission bias opposed the process. Population structure strengthens this effect because it promotes assortative mating leading to non-random associations between trait and practice. While here the process stops once the trait reaches fixation, the resulting uplift in the frequency of *E* is sufficient to significantly increase the chances of *E* becoming fixed. Niche-constructing cultural traits have effectively driven themselves to fixation. Note, the focus on a single di-allelic locus is purely for mathematical convenience, and is designed to provide insight into the likely selection on any relevant genetic variation. In reality, human biological traits are likely to be influenced by multiple genes, and the runaway cultural niche construction process described would potentially favour, and hitchhike on, any genetic variation that thrived in the resource rich environment. Moreover, genetic variation that enhances the cultural niche-constructing capability can also be caught up in this dynamic, opening up the possibility that both cultural practice and trait may experience repeated waves of selection, as is characteristic of runaway sexual selection. This process could help to explain the evolution of certain costly biological traits in the human lineage, such as large brains, complex cognition or expensive digestive enzyme production. Alleles expressed in the nervous system, brain function and brain development are an over-represented category amongst classes of genes known to be subject to recent selection (Laland *et al.* 2010; Voight *et al.* 2006; Wang *et al.* 2006). The argument of leading Evolutionary Psychologists that minds are co-adapted gene complexes that are unable to respond quickly to selection (Buss, 2008; Cosmides & Tooby, 1987; Tooby & Cosmides, 1990, 2005) must be regarded as untenable in the face of this data. Molecular geneticists have not only identified numerous brain-expressed genes in the human genome (or, indeed, no longer in the human genome) that have been subject to recent selection, they have estimated the time depth of these changes, and they have mapped them onto gene-expression networks using molecular tools such as co-expression analysis (Varki *et al.* 2008). Cultural niche construction and cultural transmission in general are prime candidates for the source of this selection (Laland *et al.* 2010; Richerson *et al.* 2010), and the processes revealed by the analysis presented here are potentially important candidate mechanisms.

Such considerations are further strengthened by the description here of the conditions favouring secondary hitch-hiking at other loci, whereby costly alleles are favoured simply because they amplify the niche-constructing effects of the cultural trait *E*. Two points stand out in these findings - firstly, that this secondary hitch-hiking can only occur when the niche-constructing effect on resource dynamics is comparatively weak, and secondly that this can only occur in spatially structured populations.

The first limitation arises from the time lag between the initial favouring of the *AAE* complex and the subsequent hitch-hiking of the *B* allele on its rising frequency. If, either because niche construction is too weak to favour allele *A*, or because niche construction is so effective that *AAE* fixes too rapidly and the resource *R* saturates, *B* cannot hitch-hike. However, within this window of opportunity, weak but nonetheless effective niche-constructing capabilities generate selection for more potent niche constructing capabilities, in a self-reinforcing dynamic.

This restriction to the range of circumstances under which secondary hitchhiking occurs results directly from the assumption of the model that there is a fixed upper bound to *R*. One might argue that for many aspects of human niche construction this assumption might be relaxed. For example, agricultural revolutions have repeatedly produced massive increases in yields per unit area. If *R* was an unbounded resource, then it is possible to envisage how a prolonged upward dynamic of primary hitchhiking resulting from niche construction could produce broader conditions favourable to the secondary hitch-hiking of enhanced niche-constructing capabilities. Nonetheless, most resources cannot rise without limit, so at some point an upper bound will be reached, and the opportunities for the evolution of more potent niche construction will diminish.

The second limitation, that secondary hitch-hiking can only occur in spatially structured populations, is especially interesting because it appears to reflect so well the kind of agriculture- or technology-driven gene-culture co-evolution discussed in the introduction. This spatial structure acts in two ways. Firstly, it generates a local concentration of the *AAE* complex, and secondly, it creates an advancing boundary zone of heterozygotes (Figure 7.1), which is especially fertile ground for secondary hitch-hiking. It is possible to envisage such zones occurring as waves of agricultural or technological innovation, through which cultural niche-constructing traits favour locally advantageous genotypes and in the process relentlessly drive their own advance, and perhaps even their own potency. In the non-spatial case, the dispersal of niche-constructing individuals across the shared resources of a population dilutes local resource concentrations, and means that statistical associations between the *A* and *B* alleles cannot build up.

The findings discussed in this chapter suggest that runaway cultural niche construction could have played an important role in human evolution, both through driving specific gene-culture coevolutionary episodes, and through facilitating the evolution of an enhanced niche-constructing capability in the human lineage through secondary hitchhiking (Laland *et al.* 2010). Note that the models presented here considered only moderate biases in cultural transmission ($0.45 \leq c \leq 0.55$), but such biases can be considerably stronger (Cavalli-Sforza & Feldman, 1981; Boyd and Richerson 1985), and this may well increase the potency of cultural niche construction further. The **B** locus in the model can potentially serve to represent any genetic locus expressed in a costly biological trait that impacts on the niche-constructing capability. Consideration of this secondary hitchhiking was largely motivated by the possibility that the average effect of allele *B* might confer a larger brain or enhanced cognitive capability. The latter includes an improved cultural capability, for instance, a capacity for motor imitation, teaching or language. Accordingly, this analysis may help to explain the observations that humans are simultaneously the species with the largest relative brain size, the most potent capacity for niche construction, and with the greatest reliance on culture. Furthermore, in spatially structured contexts, the benefits of local niche construction could potentially accrue both to the constructor's own offspring and those of its neighbours. The potential for niche-construction theory to generate insights into the evolution of cooperation is an exciting area for future research (Lehmann 2007, 2008; Van Dyken and Wade 2012).

It is apparent that cultural niche construction can lead to non-trivial alterations in evolutionary processes, especially in the case of spatially structured populations. It may be highly likely that human cultural processes have driven evolutionary episodes in the human lineage, and this analysis may help understand current features of the human genome.

SECTION 3, CHAPTER 8:

MODELS OF CULTURAL NICHE CONSTRUCTION: SELECTION AND ASSORTATIVE MATING

Material from this chapter has been submitted for publication as:

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INTRODUCTION

Niche construction has recently received attention as an important evolutionary process by which organisms alter the evolutionary pressures on themselves and organisms that share their ecological niche (Lewontin 1982; Lewontin 1983; Odling-Smee *et al*. 1996; Odling-Smee *et al.* 2003; Laland *et al.* 2003; Laland *et al.* 2010). Niche construction has usually been considered in an ecological context, and typical examples include the aeration of soil by earthworms or the building of dams by generations of beavers (Darwin 1881; Laland *et al.* 1996). These environmental changes are mediated by individual organisms and become part of the evolutionary niche into which their offspring (and those of other species) are born (Jones *et al.* 1994). In this way, organisms inherit and develop in an altered ecological niche from previous generations.

Humans have collectively engaged in millennia of niche construction on a spectacular scale, often changing their natural environment beyond recognition and almost certainly altering the course of their own evolution as a result (Laland *et al.* 2010; Richerson *et al.* 2010). Humans are also unique in the extent and complexity of their cultural learning, and recent theoretical and empirical work suggests that 'cultural niche construction,' where one set of human cultural practices contribute to the evolutionary forces acting on a second set of culturally transmitted traits, can be a powerful force explaining human evolution and behaviour (Guglielmino *et al.* 1995; Ihara and Feldman 2004; Odling-Smee and Laland 2009; Laland *et al.* 2010). Recent years have seen increasing recognition that there may be multiple levels of feedback from niche construction, including the modification of cultural selection (Laland *et al.* 2000; Odling-Smee *et al.* 2003; O'Brien and Laland *in press*). Similar ideas have been discussed in explorations of both gene-culture coevolution (Cavalli-Sforza and

Feldman 1973) and dual-inheritance theory (Feldman and Cavalli-Sforza 1976; Boyd and Richerson 1985). The model presented here follows the gene-culture and culture-culture frameworks proposed by Odling-Smee *et al.* (2003, pp. 338) and Ihara and Feldman (2004) in formulating a general model capable of accounting for both.

Culturally transmitted behavioural traits have been important in human evolution, and humans can also affect aspects of their evolutionary trajectories by influencing their cultural environment (e.g. by farming, migrating, or living in large groups). For example, the advent of dairy farming and animal domestication led, in Europe, to an increase in the frequency of the allele for lactase persistence, allowing more individuals to benefit from drinking milk into adulthood (Aoki 1986; Feldman and Cavalli-Sforza 1989; Durham 1991). Animal domestication also changed aspects of the human immune system as humans came into contact with a variety of new animal pathogens (Saunders *et al.* 2002). In this way, the human-constructed cultural niche may affect the evolutionary trajectory of genes; this is one form of niche construction first studied quantitatively by Feldman and Cavalli-Sforza (1976). However, it is also possible that one aspect of a culture or one set of culturally transmitted traits forms a cultural niche that affects either the transmission, persistence, or reproductive contributions of other cultural traits. The resulting joint evolutionary dynamics are characterised by feedbacks between the different sets of cultural entities. For example, Lipatov *et al.* (2011) describe a model that focuses on traditional Chinese marriage beliefs, which interact with the economic index of a population to influence marriage practices. This concept is sometimes called ‘context dependence’ in the social sciences, and it has received little attention from a quantitative evolutionary point of view. Cases where culturally transmitted behaviour modifies an ecological or social niche are known as ‘cultural niche construction’.

Here a model of cultural niche construction is described that formalises a wide range of evolutionary interactions, including gene-culture interactions, in which a cultural trait can alter selection pressures on a genetic trait or vice versa, and culture-culture interactions, in which a cultural trait alters the evolutionary forces acting on another cultural trait. The model can represent either type of interaction depending on the rules of transmission, mating, and selection, which generate feedback between one trait and the other (Figure 8.1). For example, the extent of assortative mating for one trait may influence the evolutionary dynamics of another. Applications of the model include the interaction between religious beliefs and fertility (e.g. Rowthorn 2011), the cultural evolution of large-scale conflict (e.g. Halperin *et al.* 2011), level of education and attitudes towards fertility control (e.g. Ihara and Feldman 2004), male-biased sex preference and marriage practices in Asia (e.g. Lipatov *et al.* 2011), or the possible interaction between marriage customs and other cultural beliefs (e.g. Brown and Feldman 2009). The model allows for two vertically transmitted traits, where each could be considered either genetically or culturally transmitted, and horizontal transmission is incorporated as cultural mutation, where an individual's traits may diverge from those of its parents. Also incorporated is assorting, an individual's tendency to choose a mate carrying the same trait (either cultural or genetic) as itself, and selection, which allows the relative fitness of the phenotypes to differ. This enables the model to elucidate the interaction between assortative mating and any direct selective advantages or disadvantages the traits might bestow. The framework accommodates two interacting cultural traits, which can influence the evolutionary trajectories of one another, but can also be applied to gene-culture interactions.

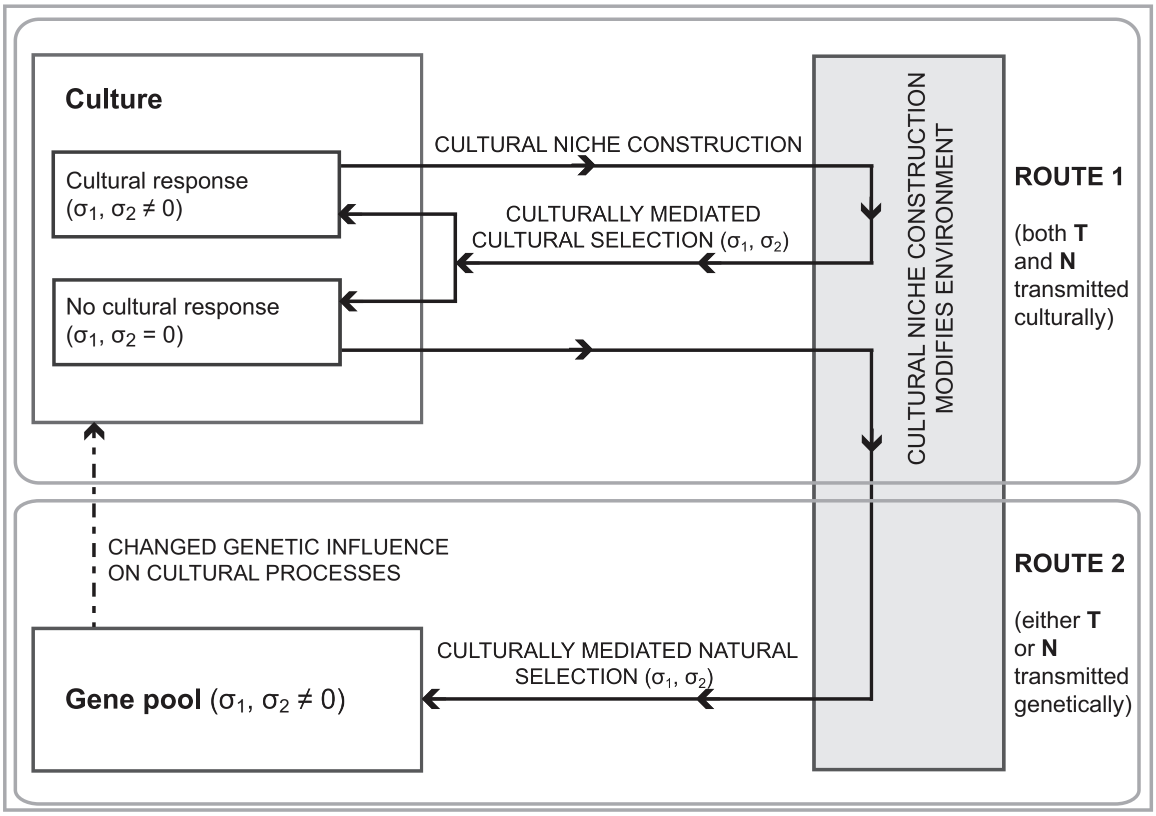

Figure 8.1. Cultural niche construction results in environmental variation, which may produce two distinct forms of feedback. Route 1: a cultural trait modifies selection pressures, which can induce further cultural change. Route 2: gene-culture coevolution, where a cultural trait changes selection pressures, causing population level genetic changes in response. Evolutionary outcomes from both route 1 and route 2 depend on the frequency of **T** and **N (**cultural or genetic) traits in the population and the selection pressures they generate, here represented by σ_i. Modified from Odling-Smee, Laland, and Feldman (2003).

THE MODEL

The model considers two cultural traits: **T,** a recipient trait that determines a cultural phenotype, and **N,** a niche constructing trait that determines selection and assortative mating parameters that influence the dynamics of the **T** trait. Each has two possible states (**T**: *T*, *t* and **N**: *N*, *n*), thus there are four possible phenotypes – *TN* (type 1), *Tn* (type 2), *tN* (type 3), and *tn* (type 4), whose population frequencies are denoted by x_1, x_2, x_3, and x_4, respectively, with $\sum_{i=1}^{4} x_i = 1$. The relative fitnesses of *T* and *t* individuals depend on the state of the **N** trait, as shown in Table 8.1. Individuals with the *t* trait always have a relative fitness equal to 1, but the relative fitnesses of *TN* and *Tn* can differ. The state of the **N** trait sets the value of the selection coefficient σ_i ($-1 \leq \sigma_i \leq 1$), such that the phenotype *TN* has fitness $1 + \sigma_1$ and the phenotype *Tn* has fitness $1 + \sigma_2$,, whereas the *tN* and *tn* phenotypes both have fitness 1.

Table 8.1. Relative fitnesses of the four phenotypes.

Phenotype	Relative fitness
TN	$1 + \sigma_1$
Tn	$1 + \sigma_2$
tN	1
tn	1

The relative fitness of individuals carrying the *T* trait can differ from that of individuals carrying the *t* trait. The amount of this difference is dictated by the **N** state: the *N* trait confers a fitness difference of σ_1 between *TN* and *tN*, and the *n* trait confers a fitness difference of σ_2 between *Tn* and *tn*.

The state of the **N** trait also determines the value of an assortative mating parameter, which measures the departure from random mating. A 'choosing parent,' is arbitrarily assigned as the father in the subsequent analysis. The choosing parent's **N** state dictates the level of assortative mating, that is, the degree to which an individual of a given **T** state will preferentially mate with another individual of the same state, expressed by parameters α_i ($0 \leq \alpha_i \leq 1$). In the population, a fraction ($1 - \alpha_i$) of individuals will mate randomly, while the remainder of the population (α_i) will mate preferentially with individuals of the same **T** state. If the choosing parent is *N*, individuals mate randomly with probability $1 - \alpha_1$ and mate preferentially with individuals of the same **T** state with probability α_1, whereas if the choosing parent is *n*, individuals mate randomly with probability $1 - \alpha_2$ and mate preferentially with individuals of the same **T** state with probability α_2.

Table 8.2. Mating frequencies for all possible matings.

♂ x ♀	mating frequency	♂ x ♀	mating frequency
TN x *TN*	$m_{1,1} = x_1^2(1-\alpha_1) + \frac{\alpha_1 x_1^2}{(x_1 + x_2)}$	*tN* x *TN*	$m_{3,1} = x_3 x_1(1-\alpha_1)$
TN x *Tn*	$m_{1,2} = x_1 x_2(1-\alpha_1) + \frac{\alpha_1 x_1 x_2}{(x_1 + x_2)}$	*tN* x *Tn*	$m_{3,2} = x_3 x_2(1-\alpha_1)$
TN x *tN*	$m_{1,3} = x_1 x_3(1-\alpha_1)$	*tN* x *tN*	$m_{3,3} = x_3^2(1-\alpha_1) + \frac{\alpha_1 x_3^2}{(x_3 + x_4)}$
TN x *tn*	$m_{1,4} = x_1 x_4(1-\alpha_1)$	*tN* x *tn*	$m_{3,4} = x_3 x_4(1-\alpha_1) + \frac{\alpha_1 x_3 x_4}{(x_3 + x_4)}$
Tn x *TN*	$m_{2,1} = x_1 x_2(1-\alpha_2) + \frac{\alpha_2 x_1 x_2}{(x_1 + x_2)}$	*tn* x *TN*	$m_{4,1} = x_4 x_1(1-\alpha_2)$
Tn x *Tn*	$m_{2,2} = x_2^2(1-\alpha_2) + \frac{\alpha_2 x_2^2}{(x_1 + x_2)}$	*tn* x *Tn*	$m_{4,2} = x_4 x_2(1-\alpha_2)$
Tn x *tN*	$m_{2,3} = x_2 x_3(1-\alpha_2)$	*tn* x *tN*	$m_{4,3} = x_4 x_3(1-\alpha_2) + \frac{\alpha_2 x_4 x_3}{(x_3 + x_4)}$
Tn x *tn*	$m_{2,4} = x_2 x_4(1-\alpha_2)$	*tn* x *tn*	$m_{4,4} = x_4^2(1-\alpha_2) + \frac{\alpha_2 x_4^2}{(x_3 + x_4)}$

In this model, α_1 is the rate of assortment if the choosing parent is *N,* and α_2 is the rate of assortment if the choosing parent is *n*. The choosing parent is listed first for each mating. On the right side of the equations, the first term represents the frequency of random matings and the second term the frequency of assortative matings.

There are sixteen father-mother pairs possible from the four phenotypes described here, denoted by notation $m_{i,j}$ to indicate the frequency of a mating between a father of type *i* and a mother of type *j* where $i, j = \{1, 2, 3, 4\}$; the mating frequency of each pairing is given in Table 8.2. With preferential mating based on their **T** state, the mating frequency for individuals of different **T** states is the product of the frequency of each phenotype multiplied by the probability of individuals mating at random (1 - α_i). The mating frequency for individuals of the same **T** state is the sum of the probability that the individuals mate at random and the probability that the individuals mate assortatively. Since the traits in question are transmitted vertically, for each phenotype it is psossible to specify the probability that the mating produces an offspring of that phenotype. These probabilities, b_i and c_i for $i = \{0, 1, 2, 3\}$ shown in Table 8.3, are assumed to be constant ($0 \leq b_i \leq 1$, $0 \leq c_i \leq 1$).

Table 8.3. Probabilities of offspring outcomes from cultural trait pairings

	T	t		N	n
$T \text{ x } T$	b_3	$1-b_3$	$N \text{ x } N$	c_3	$1-c_3$
$T \text{ x } t$	b_2	$1-b_2$	$N \text{ x } n$	c_2	$1-c_2$
$t \text{ x } T$	b_1	$1-b_1$	$n \text{ x } N$	c_1	$1-c_1$
$t \text{ x } t$	b_0	$1-b_0$	$n \text{ x } n$	c_0	$1-c_0$

For each mating, the probability of transmitting each trait is given. For example, a mating between a *T* individual and another *T* individual will result in a T offspring with probability b_3 and a *t* offspring with probability ($1 - b_3$).

T and **N** are assumed to be transmitted independently, so the probability of offspring outcomes for each of the sixteen possible matings is obtained by multiplying the corresponding probabilities from each side of Table 3. For example, a mating of a *TN* individual with a *Tn* individual will produce a *TN* offspring with probability $b_3\, c_2$ and a *Tn* offspring with probability $b_3\,(1 - c_2)$. If $b_0 = 0$ and $b_3 = 1$, then there is no cultural 'mutation' from one **T** state to another: two *T* parents will always produce a *T* offspring and two *t* parents will always produce a *t* offspring. In addition, these transmission parameters could take values that represent Mendelian inheritance: $b_0 = 0$, $b_1 = b_2 = 0.5$, and $b_3 = 1$. However, if $b_0 > 0$ and $b_3 < 1$, there is some rate at which two *T* parents can produce *t* offspring and vice versa. The corresponding statements are true of c_i with respect to the **N** state. This cultural mutation may also be viewed as frequency-independent horizontal transmission.

To compute the frequency of a given phenotype in the next generation, each mating frequency is multiplied by the probability that the mating produces that offspring phenotype and sum over each of the sixteen possible mating combinations. Selection, in terms of σ_1 and σ_2, then operates on these offspring. The full recursions, giving x_i', the phenotype frequencies in the next generation, in terms of x_i in the current generation, are given in Equations 8.1-8.4 below.

$$
\begin{gathered}
\bar{w}x_1' = (1+\sigma_1)(m_{1,1}b_3c_3 + m_{1,2}b_3c_2 + m_{1,3}b_2c_3 + m_{1,4}b_2c_2 + m_{2,1}b_3c_1 + m_{2,2}b_3c_0 + \\
m_{2,3}b_2c_1 + m_{2,4}b_2c_0 + m_{3,1}b_1c_3 + m_{3,2}b_1c_2 + m_{3,3}b_0c_3 + m_{3,4}b_0c_2 + m_{4,1}b_1c_1 + \\
m_{4,2}b_1c_0 + m_{4,3}b_0c_1 + m_{4,4}b_0c_0)
\end{gathered}
$$

(8.1)

$$
\begin{gathered}
\bar{w}x_2' = (1+\sigma_1)(m_{1,1}b_3(1-c_3) + m_{1,2}b_3(1-c_2) + m_{1,3}b_2(1-c_3) + m_{1,4}b_2(1-c_2) + \\
m_{2,1}b_3(1-c_1) + m_{2,2}b_3(1-c_0) + m_{2,3}b_2(1-c_1) + m_{2,4}b_2(1-c_0) + m_{3,1}b_1(1-c_3) + \\
m_{3,2}b_1(1-c_2) + m_{3,3}b_0(1-c_3) + m_{3,4}b_0(1-c_2) + m_{4,1}b_1(1-c_1) + m_{4,2}b_1(1-c_0) + \\
m_{4,3}b_0(1-c_1) + m_{4,4}b_0(1-c_0))
\end{gathered}
$$

(8.2)

$$
\begin{gathered}
\bar{w}x_3' = (m_{1,1}(1-b_3)c_3 + m_{1,2}(1-b_3)c_2 + m_{1,3}(1-b_2)c_3 + m_{1,4}(1-b_2)c_2 + \\
m_{2,1}(1-b_3)c_1 + m_{2,2}(1-b_3)c_0 + m_{2,3}(1-b_2)c_1 + m_{2,4}(1-b_2)c_0 + m_{3,1}(1-b_1)c_3 + \\
m_{3,2}(1-b_1)c_2 + m_{3,3}(1-b_0)c_3 + m_{3,4}(1-b_0)c_2 + m_{4,1}(1-b_1)c_1 + m_{4,2}(1-b_1)c_0 + \\
m_{4,3}(1-b_0)c_1 + m_{4,4}(1-b_0)c_0)
\end{gathered}
$$

(8.3)

$$\begin{aligned}\bar{w}x_4' = {} & (m_{1,1}(1-b_3)(1-c_3)+m_{1,2}(1-b_3)(1-c_2)+m_{1,3}(1-b_2)(1-c_3)+m_{1,4}(1-b_2)(1-c_2)+ \\ & m_{2,1}(1-b_3)(1-c_1)+m_{2,2}(1-b_3)(1-c_0)+m_{2,3}(1-b_2)(1-c_1)+m_{2,4}(1-b_2)(1-c_0)+ \\ & m_{3,1}(1-b_1)(1-c_3)+m_{3,2}(1-b_1)(1-c_2)+m_{3,3}(1-b_0)(1-c_3)+m_{3,4}(1-b_0)(1-c_2)+ \\ & m_{4,1}(1-b_1)(1-c_1)+m_{4,2}(1-b_1)(1-c_0)+m_{4,3}(1-b_0)(1-c_1)+m_{4,4}(1-b_0)(1-c_0))\end{aligned} \tag{8.4}$$

The average fitness ($\bar{w}$) is the sum of the right side these four equations and acts to normalise x_i' so that $\sum_i x_i' = 1$. If $x_i' = x_i$, for i = {1, 2, 3, 4}, the system is at equilibrium and the number and structure of these equilibria, as well as whether they are stable, depend on the values of the parameters in Tables 8.1-8.3. This analysis of the model is then combined with numerical iterations to explore the parameter space ($-1 \leq \sigma_i \leq 1$, $0 \leq \alpha_i \leq 1$, $0 \leq b_i \leq 1$, $0 \leq c_i \leq 1$) and the nature and stability of the equilibria of the system. For a given set of parameter values, the system is iterated until convergence, from several initial values of x_i and the equilibrium approached from each can be examined.

RESULTS

Three sets of parameters interact in this model: the selection parameters σ_i, assortative mating parameters α_i, and vertical cultural transmission parameters, b_i and c_i. The values of both σ_i and α_i are determined by an individual's **N** state, as described above. In order to study the dynamics of a population with a given set of parameter values, the possible equilibria, their stability, and the effect of initial phenotype frequencies on the eventual equilibrium reached are investigated. Although some special cases are amenable to mathematical solution, most require numerical analysis. For a given set of parameters, the frequency of each phenotype (x_1, x_2, x_3, and x_4) is represented as a point in the tetrahedron shown in Figures 8.2-8.4, with a vertex representing the fixation of a phenotype; for example, $x_1 = 1$ at the vertex labeled *TN*. Likewise, a point on the edge between the vertices labeled *tN* and *tn* represents $x_1 = x_2 = 0$. Arrows inside the tetrahedron begin at initial frequencies of each phenotype and point in the direction of the equilibrium approached from these starting frequencies after 50,000 generations.

Case 1: No selection, no assortative mating no cultural mutation

Here $\sigma_1 = \sigma_2 = 0$ (no selection), $\alpha_1 = \alpha_2 = 0$ (no assortative mating), $b_0 = 0$, $b_3 = 1$ (no cultural mutation of the **T** state), and $c_0 = 0$, $c_3 = 1$ (no cultural mutation of the **N** state). The parameters b_1 and b_2 are the probabilities of producing a *T* offspring from a *T* x *t* or a *t* x *T* mating, respectively, and in general these parameters need not be equal. Likewise, c_1 and c_2 correspond to the probability of producing an offspring with an *N* trait from an *N* x *n* or an *n* x *N* mating, respectively. The balance of $(b_1 + b_2)$ with $(c_1 + c_2)$ dictates the eventual fixation: if $b_1 + b_2 \neq 1$ and $c_1 + c_2 \neq 1$, the system approaches fixation of a single phenotype. For example, if $b_1 + b_2 > 1$, more offspring with the *T* trait are produced from mixed *T*/*t* matings than offspring with the *t* trait. If $c_1 + c_2 > 1$ as well, then more *N* offspring are produced from mixed *N*/*n* matings than *n* offspring. If both inequalities hold, *TN* will be favoured in the long term, and any initial phenotype frequencies such that $0 < x_1, x_2, x_3, x_4 < 1$ will evolve toward $x_1 = 1$. However, if *N* is initially absent in the population, the population approaches fixation in *Tn* (Figure 8.2a). If $b_1 + b_2 = 1$ and $c_1 + c_2 = 1$, no phenotype is favoured by vertical transmission, and any starting point such that $0 < x_1, x_2, x_3, x_4 < 1$ can be an equilibrium. This is referred to as the neutral case.

If $c_1 + c_2 = 1$, which is typical of Mendelian inheritance but is also possible with cultural transmission, then neither *N* nor *n* will be favoured and both will be present at equilibrium. For example, if $c_0 = 0$, $c_1 = 0.6$, $c_2 = 0.4$, and $c_3 = 1$, then if $b_1 + b_2 > 1$ the T

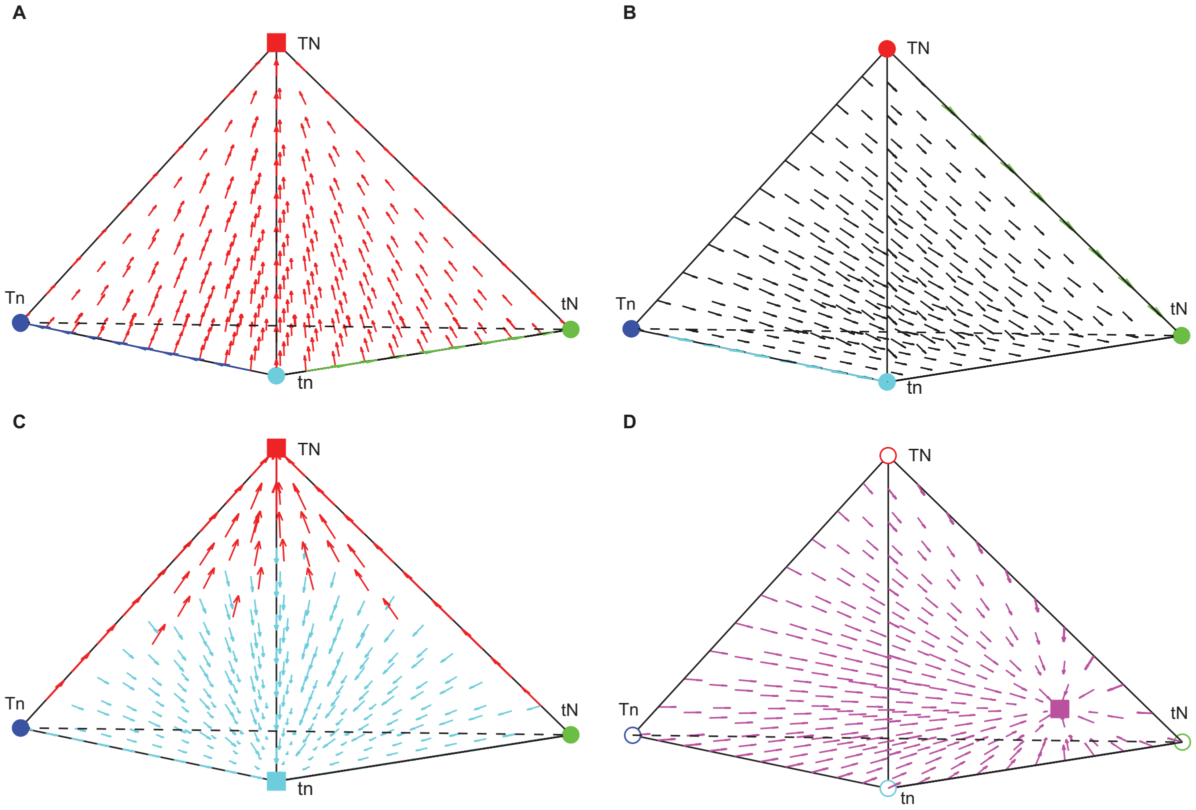

Figure 8.2. In this and subsequent figures, a filled square at a vertex indicates a stable fixation at that vertex. A filled circle indicates an equilibrium that is unstable except in a specific hyperplane. Inside the tetrahedron, arrows originate at the population's initial phenotype frequencies and point toward the equilibrium. Arrows are color-coded by the phenotype fixed at the resulting equilibrium (*Tn*: red, *Tn*: blue, *tN*: green, *tn*: cyan, *tN*-*tn* edge: black). (A) No selection, no assortative mating, no cultural mutation: when b_1+b_2>1 and c_1+c_2>1, *TN* vertex is stable. When 0<α_1, α_2<1, the same vertex is stable. (B) No selection, no assortative mating, no cultural mutation: when b_1+b_2<1, *t* approaches fixation, if c_1+c_2=1, *N* and *n* persist in initial proportions. Any point along the edge connecting the *tn* and *tN* vertices can be an equilibrium. (C) Selection but no assortative mating, no cultural mutation. For certain parameters, cultural transmission favours fixation of one phenotype but selection favours another. In some cases, two points are stable and which is approached depends on initial frequencies. In the case shown here, α_1=α_2=0, b_0=c_0=0, b_3=c_3=1, b_1=0.8, b_2=0.5, c_1=0.5, c_2=0.2, σ_1=-0.2, and σ_2=-0.6. Transmission favours *T* and *n*, but *Tn* is selected against, so the population approaches fixation of either *TN* or *tn* depending on initial frequencies. (D) Assortative mating, selection, and cultural mutation. From all initial phenotype frequencies, the population will approach a single stable polymorphism. In this case, α_1=0.1, α_2=0.1, b_0=0.05, b_1=0.49, b_2=0.52, b_3=0.95, c_0=0.05, c_1=0.51, c_2=0.53, c_3=0.95, σ_1=-0.2, and σ_2=-0.1. At equilibrium, x_1≈0.1438, x_2≈0.0492, x_3≈0.6262, and x_4≈0.1808.

state will approach fixation and if $b_1 + b_2 < 1$ the t state will approach fixation, but in both cases N and n will remain at their original proportions in the population (Figure 8.2b). In this case, the **N** trait is neutral. Corresponding statements are true for the T and t states if $b_1 + b_2 = 1$. If both $b_1 + b_2 = 1$ and $c_1 + c_2 = 1$, then both the **T** and the **N** traits are neutral, and T, t, N, and n will persist in their initial proportions. Note that while the proportions of these individual states will remain constant, the phenotype frequencies (x_1, x_2, x_3, and x_4) can change from their initial values because offspring can inherit their **T** and **N** traits from different parents.

Case 2: No selection, assortative mating, no cultural mutation

With $\sigma_1 = \sigma_2 = 0$ (no selection), α_1, $\alpha_2 > 0$ (assortative mating), $b_0 = c_0 = 0$ and $b_3 = c_3 = 1$ (no cultural mutation), the dynamics are largely similar to those in Case 1 in that the transmission parameters dictate which phenotype ultimately reaches fixation (Figure 8.2a) unless there is complete assortative mating, in which case the values of the parameters b_1 and b_2 are irrelevant. Thus, when $\alpha_1 = \alpha_2 = 1$, c_1 and c_2 dictate which of the **N** states will approach fixation and the **T** state is neutral. For example, if $c_1 + c_2 < 1$, n will approach fixation, but any proportions of Tn and tn can be an equilibrium. Here, the Tn-tn edge of the tetrahedron is neutrally stable; perturbing the system away from this edge by adding N individuals to the population will result in a return to this edge. The proportions of T and t will not change from generation to generation, but if a perturbation changes these proportions, they will remain at the perturbed frequencies. Likewise, if $c_1 + c_2 > 1$, the edge between the TN and tN vertices will be stable when assortative mating is complete.

Case 3: Selection, no assortative mating, no cultural mutation

Next, the case in which the fitnesses of the phenotypes are not equal, individuals mate randomly, and there is no cultural mutation is considered: $-1 < \sigma_1, \sigma_2 < 1$, $\sigma_1 \neq \sigma_2$, $\alpha_1 = \alpha_2 = 0$ (no assortative mating), and $b_0 = c_0 = 0$ and $b_3 = c_3 = 1$ (no cultural mutation). In this case, a single phenotype often approaches fixation. However, when vertical transmission favours one phenotype but selection favours another, two vertices may be locally stable, in which case the initial phenotype frequencies dictate which vertex will eventually be approached (Figure 8.2c).

Case 4: Selection, assortative mating, cultural mutation

When there is cultural mutation in the population ($0 < b_i, c_i < 1$), no boundary can be reached from any starting point. In all cases examined, only one stable polymorphism exists in the interior of the tetrahedron (Figure 8.2d).

Case 5: Selection, assortative mating, no cultural mutation

With both selection and assortative mating ($-1 < \sigma_1, \sigma_2 < 1$, $\alpha_1, \alpha_2 > 0$) but no cultural mutation ($b_0 = c_0 = 0$, $b_3 = c_3 = 1$), stable equilibria with one or both traits fixed are possible. In most such cases, a single phenotype is favoured and ultimately approaches fixation, except in populations that are initially missing one of these traits. Approximately 25 million combinations of parameters were simulated, avoiding values close to zero or one ($0.2 < \alpha_1, \alpha_2 < 0.8$, $0.2 < b_1, b_2 < 0.8$, $0.2 < c_1, c_2 < 0.8$, $-0.8 < \sigma_1, \sigma_2 < 0.8$) and found that in a small fraction of cases (on the order of 1 in 50,000), multiple stable equilibria are possible, including one vertex and one polymorphism with all phenotypes at a frequency greater than 0.01, as well as at least one unstable equilibrium. Using these rare polymorphisms as starting points, it was possible to identify patterns of parameter values that allowed for the persistence of all four phenotypes. As an illustration, consider the case where $\alpha_1 = 0.8$, $\alpha_2 = 0.3$, $b_0 = 0$, $b_1 = 0.7$, $b_2 = 0.7$, $b_3 = 1$, $c_0 = 0$, $c_1 = 0.5$, $c_2 = 0.2$, $c_3 = 1$, $\sigma_1 = -0.2$, and $\sigma_2 = -0.7$. Testing numerous combinations of b_1 and b_2 but holding the other parameters constant, it can be shown that a subset of these combinations produce a stable polymorphism and the remainder give fixation of a single phenotype (Figure 8.3a); likewise, a subset of c_1 and c_2 pairs will result in the stable persistence of all four phenotypes (Figure 8.3b).

In cases where multiple stable equilibria exist, the equilibrium approached depends on the population's initial composition. For example, with the set of parameters listed above, an interior stable polymorphism exists, and from outside of its domain of attraction the population approaches fixation of one phenotype (Figure 8.3c). Which phenotype approaches fixation depends on the relationship between the parameters. For example, if $\alpha_2 > \alpha_1$, $c_1 + c_2 > 1$, $\sigma_2 > \sigma_1$, $\sigma_1 < 0$, and $\sigma_2 < 0$, then that $x_3 = 1$ tends to be locally stable in addition to the stable polymorphism. Similarly, when $\alpha_1 > \alpha_2$, $c_1 + c_2 < 1$, $\sigma_1 > \sigma_2$, $x_4 = 1$ is likely to be stable in addition to the stable polymorphism. In both of these situations there is one unstable fixation and another unstable equilibrium between the polymorphism's domain of attraction and the stable fixation point.

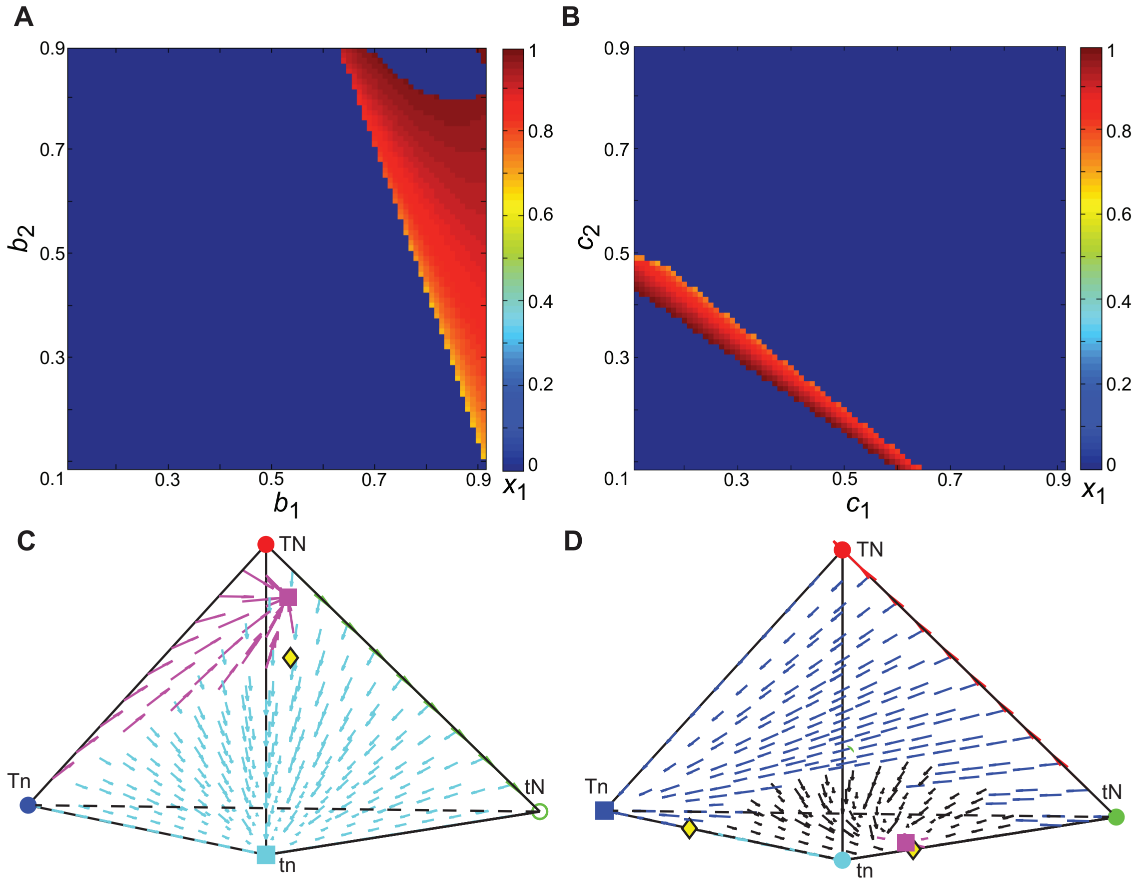

Figure 8.3. For most parameter sets, the population approaches a single vertex; in rare cases a stable polymorphism is also present. Panels (A)-(C) show the parameter values α_1=0.8, α_2=0.3, b_0=0, b_1=0.7, b_2=0.7, b_3=1, c_0=0, c_1=0.5, c_2=0.2, c_3=1, σ_1=-0.2, σ_2=-0.7, (A)-(B) shows varied pairs of transmission parameters. (A) Effect of transmission of ***T*** on the presence of a polymorphism. The x-axis represents the value of b_1, y-axis represents the value of b_2, and the colour scale shows the value of x_1. (B) Effect of transmission of ***N*** on the presence of a polymorphism. The x-axis represents the value of c_1, the y-axis represents the value of c_2, and the colour scale represents the value of x_1. (C) Pink square represents a stable polymorphism ($x_1 \approx 0.814$, $x_2 \approx 0.0162$, $x_3 \approx 0.0937$, $x_4 \approx 0.0763$). Pink arrows illustrate the domain of attraction of this equilibrium. Yellow diamonds represent an unstable equilibrium between the domains of attraction of the polymorphism and the *tn* vertex. (D) Polymorphism where $c_1 + c_1 = 1$. For some initial frequencies, the population approaches a single fixed point at the blue square. Pink square represents a stable polymorphic internal equilibrium, pink arrows illustrate the domain of attraction of this equilibrium. Red, green, and cyan circles and yellow diamonds represent unstable equilibria. Black arrows begin at initial conditions that result in an equilibrium on the *tN*-*tn* edge of the tetrahedron. Yellow diamonds show unstable equilibria on the *n* and *t* fixation edges. In this case, α_1=0.8, α_2=0.3, b_0=0, b_1=0.2, b_2=0.3, b_3=1, c_0=0, c_1=0.3, c_2=0.7, c_3=1, σ_1=0.2, and σ_2=0.4.

In certain cases, parameter combinations can produce quite complex outcomes, especially when the cultural transmission parameters from mixed matings sum to one for one trait: from certain initial frequencies a stable interior polymorphism is approached, whereas from other initial frequencies, fixation in one phenotype is approached, while other starting points are neutral with respect to one of the traits (an edge of the tetrahedron). In Figure 8.3d, for example, with $\alpha_1 = 0.8$, $\alpha_2 = 0.3$, $b_0 = 0$, $b_1 = 0.2$, $b_2 = 0.3$, $b_3 = 1$, $c_0 = 0$, $c_1 = 0.3$, $c_2 = 0.7$, $c_3 = 1$, $\sigma_1 = 0.2$, and $\sigma_2 = 0.4$, *Tn* fixation ($x_2 = 1$) is locally stable, and there is a stable polymorphism with all four phenotypes present ($x_1 \approx 0.0176$, $x_2 \approx 0.0284$, $x_3 \approx 0.2558$, and $x_4 \approx 0.6981$). In addition, there are four unstable equilibria: two distinct fixation points (*TN* can approach fixation when *n* is completely absent and *tn* can approach fixation when *N* is completely absent and $x_2 < 0.643$), one point between the domains of attraction of the stable polymorphism and the neutral edge, and one point between the domains of attraction of the *Tn* vertex and the *tn* vertex. Further, the domain of attraction of the neutral edge does not include all initial phenotype frequencies near it. If the initial conditions are close to fixation in *t*, that is, $x_1 + x_2 << x_3 + x_4$ but all $x_i > 0$, the system will approach different equilibria depending on the initial proportions of *N* and *n* in the population. For example, with the parameters above, if $x_3 > 0.735$ initially, the population will approach fixation at $x_2 = 1$, but if $x_3 < 0.735$ initially, the population will approach an equilibrium in which x_3 and x_4 are both present. For most initial frequencies with $x_3 < 0.735$, $x_3 + x_4 = 1$ at equilibrium, but there is a set of initial conditions near the *tN*-*tn* edge, where $0.261 < x_3 < 0.372$ and x_1 and x_2 are close to zero, that lead to an equilibrium with all four phenotypes present. This example illustrates that a single set of parameters for selection, assortative mating, and cultural transmission can result in a diverse set of evolutionary outcomes depending on the founding history of the population.

Case 6: Gene-culture coevolution

Finally, the case in which individuals can mate assortatively and the fitnesses of the phenotypes are not equal ($-1 < \sigma_1, \sigma_2 < 1, \sigma_1 \neq \sigma_2, \alpha_1, \alpha_2 > 0$) but one of the traits follows Mendelian transmission rules can be considered. Thus, a culturally transmitted trait is modifying the evolution of a genetically inherited trait or vice versa. In this case, the genetically transmitted trait often approaches fixation, and the culturally transmitted trait tends to approach fixation or an equilibrium between the two cultural phenotypes. However, with certain levels of selection and assorting, a culturally inherited trait (**N**) can modify the evolutionary dynamics of a genetic trait (**T**), resulting in the stable persistence of all four phenotypes. Likewise, a genetically inherited trait (**N**) can modify the evolution of a cultural trait (**T**) to produce a polymorphism. These polymorphisms can be found in cases with and without cultural mutation of the culturally transmitted trait. In contrast, if both traits exhibit Mendelian inheritance, no combination of assorting and selection appear to result in a polymorphism where all four genotypes are present in the population: at least one set of non-Mendelian transmission parameters seems to be necessary for a polymorphic equilibrium. By varying the transmission, selection, and assorting parameters in turn while maintaining Mendelian inheritance of one trait, regions of the parameter space that result in the persistence of all four phenotypes are found, but only when the transmission of the other trait is non-Mendelian (Figure 8.4).

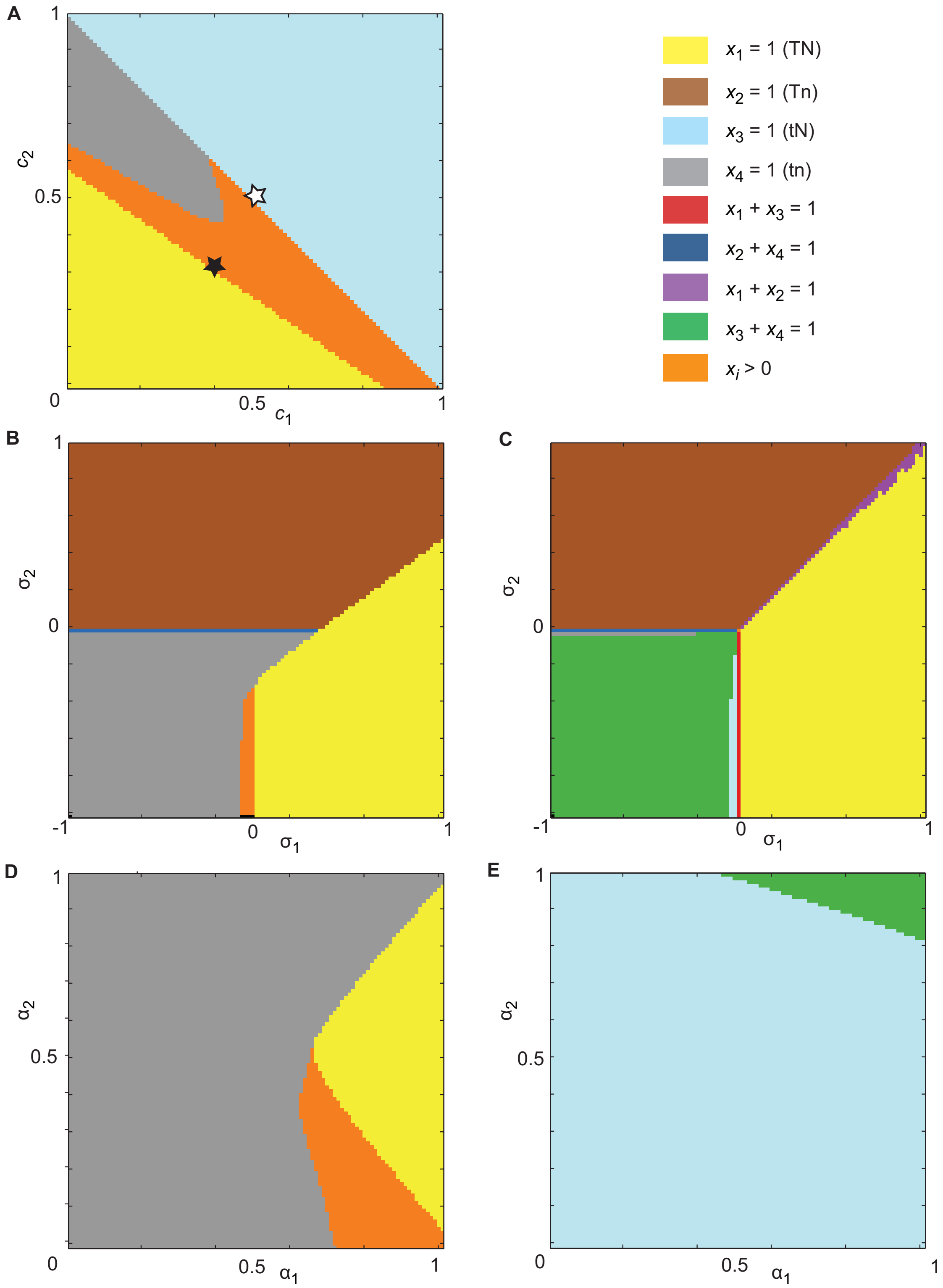

Figure 8.4.When the **T** trait is transmitted by Mendelian inheritance and the **N** trait is transmitted culturally, assorting and selection may lead to gene-culture polymorphisms. Parameter set α_1=0.83, α_2=0.24, b_0=0, b_1=b_2=0.5, b_3=1, c_0=0, c_3=1, σ_1=-0.01, and σ_2=-0.82 and varied pairs of parameters as indicated. (A) Cultural transmission affects equilibria: c_1 and c_2 varied between 0 and 1, and the

equilibrium approached from initial frequencies near the x_1-x_2 edge is indicated by colour. Polymorphisms exist in the orange region. In (B) and (D), the transmission parameters are indicated by the black star in (A): c_1=0.4 and c_2=0.31. In (C) and (E), the Mendelian transmission parameters indicated by the white star in (A) were used: c_1=0.5 and c_2=0.5. (B) Selection parameters that produce a polymorphism are shown in orange. (C) When both traits show Mendelian transmission, no stable polymorphisms exist for any combination of selection levels. (D) The assorting parameter combinations that produce a gene-culture polymorphism are shown in orange. (E) When both traits show Mendelian transmission, polymorphisms do not exist for any combination of assorting parameters.

DISCUSSION

The term ‘cultural niche construction’ potentially encompasses at least two types of interactive processes (Odling-Smee *et al.* 2003). In culture-culture interaction, a cultural trait changes the selection pressures on, or transmissibility of, other cultural traits. The other is a process generating feedback between cultural evolution and genetic evolution leading to gene-culture coevolution (Laland *et al.* 2000). The model presented above can represent either of these processes depending on the choice of transmission parameters. The feedback in the model is generated through the interaction of the selection parameters σ_i, the assorting rates α_i, and the transmission rates b_i and c_i. The **T** and **N** traits can be culturally transmitted, and **N** affects the relative fitnesses of *T* and *t* (see Table 8.1). The **N** trait thus affects the evolution of the population as a result of its culturally induced effect on the **T** trait. This is cultural niche construction, the strength and characteristics of which depend on all three sets of parameters in this model: the transmission parameters, the selection pressures, and the levels of assortative mating.

Our model, indeed, has applicability that extends beyond cultural niche construction since it can represent gene-culture coevolution in either of two contexts: a genetically inherited trait that modifies the evolution of a culturally inherited trait, and vice versa. When one of the two traits exhibits Mendelian inheritance (for example, $b_0 = 0$, $b_1 = b_2 = 0.5$, $b_3 = 1$) and the other is not Mendelian, most combinations of cultural transmission, selection, an assorting lead to equilibria in which the genetically inherited trait is fixed. However, as with two culturally transmitted traits (Case 5), the transmission, assorting, and selection can be balanced in such a way as to result in stable polymorphisms of all four phenotypes. Either case of gene-culture coevolution may result in polymorphisms if the cultural transmission, selection, and assorting interact appropriately. This phenomenon is seen both when the cultural mutation is present and when it is absent. However, no combination of assorting and selection parameters were found to give stable polymorphisms when both **T** and **N** were inherited according to Mendelian rules. This underscores the evolutionary importance of the interaction between cultural transmission, selection, and assorting. The model may be applied to a wide range of cultural niche construction systems, including three often studied social applications: the cultural evolution of religion and high fertility, the cultural evolution of war, and the cultural evolution of sex ratio bias, which is strong in several parts of the world and can interact with mating customs (Li *et al.* 2001).

Cultural evolution of religion and fertility

The cultural evolution of religious belief and its effects on in- and out-group acceptance and conflict have been widely studied, and attempts have been made to explain the evolution of both the human capacity for religious acceptance and its persistence as a cultural belief (Rowthorn et al 2011; Sosis and Alcorta 2003; Henrich 2009). The interaction between religiosity and fertility discussed by Rowthorn (2011) can also be described by the model presented here, although there are some fundamental differences between his model and this one. After Rowthorn (2011), it is possible to suppose that one of the traits controls a genetic predisposition to religiosity (**N**) and the other determines the cultural belief in religion (**T**). Following Rowthorn's assumptions that there is complete assortative mating according to religious belief, **T**, ($\alpha_1 = \alpha_2 = 1$). The **N** trait is transmitted genetically, that is, $c_0 = 0$, $c_3 = 1$, and $c_1 = c_2 = 0.5$. The complete assortative mating renders the parameters b_1 and b_2 irrelevant since a *T* individual will not mate with a *t* individual. In his model, Rowthorn (2011) includes parameters controlling what he describes as 'switching;' these are the probabilities that an individual adopts the opposite state of the cultural trait from the phenogenotype inherited through vertical transmission. In his model, there are four such switching parameters, one for each phenotype. Switching from non-belief (n) to religious belief (r) is considered more likely for an individual possessing the religiosity allele (R) than the non-religiosity allele (N), and, likewise, switching to non-belief is more likely for an individual with the non-religiosity allele. Rowthorn assumes $s_R^n \geq s_N^n$ (where s_R^n represents the probability that an individual of phenotype *nR* will switch to *rR*, and so on) and $s_R^r \leq s_N^r$; in other words, the religiosity gene predisposes individuals to religious belief because the probability of switching to religious belief, from *n* to *r*, is greater for individuals carrying *R* and vice versa for carriers of *N*. Note, one contentious aspect of Rowthorn's model is that the transmission does not involve conversion by contact with individuals of another type (horizontal transmission as defined by Cavalli-Sforza and Feldman (1981)), but occurs at a constant rate for each phenotype: it is not frequency dependent and can be viewed as mutation rather than cultural transmission.

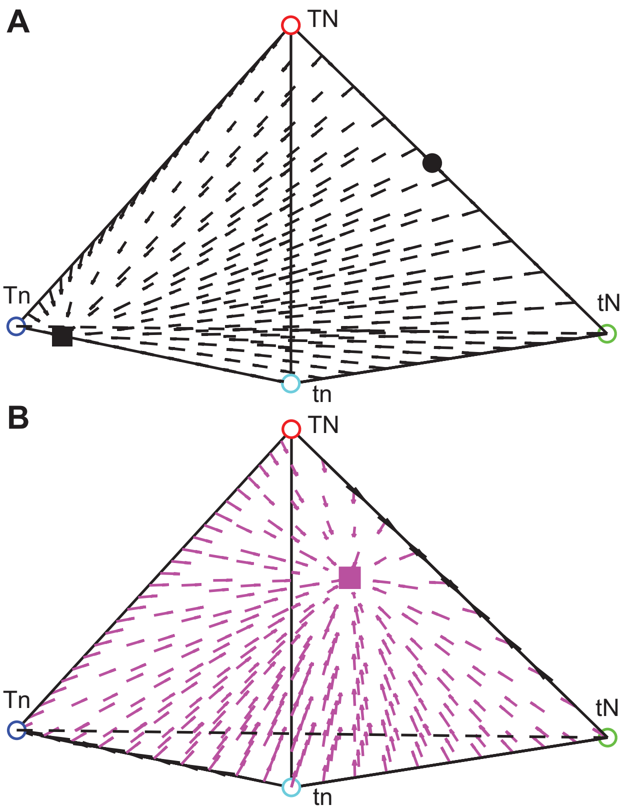

Figure 8.5. Small fitness differences can alter the evolutionary dynamics of cultural traits. **N** represents the genetically transmitted religious predisposition trait and **T** represents the culturally transmitted belief trait. For both panels, α_1=0.73, α_2=0.94, b_0=0.02, b_1=0.3, b_2=0.31, b_3=0.98, c_0=0, c_1=c_2=0.5, and c_3=1. (A) When σ_1=σ_2=0.12, a stable equilibrium exists on the *Tn*-*tn* edge (black square), i.e. fixation of the non-religiosity allele (*n*) and a polymorphism between religious belief (*T*) and non-belief (*t*), which is approached from all starting points except those on the *TN*-*tN* edge, which approach the equilibrium illustrated by the black circle. (B) When σ_1=0.12 and σ_2=0.11, a stable polymorphism (pink square) exists such that both religious and non-religious predispositions, as well as religious belief and non-belief, coexist in the population (x_1≈0.521, x_2≈0.127, x_3≈0.295, x_4≈0.057).

Rowthorn's condition $s_R^n \geq s_N^n$ and $s_R^r \leq s_N^r$ cannot be matched exactly in the model presented here, where transmission of **T** is independent of transmission of **N**, so the probability of cultural mutation depends on the frequencies of the relevant states, which can change over time and with different initial frequencies. For example, the frequency of a cultural mutation from *T* to *t* is the total frequency of *T* x *T* matings in the population (when $\alpha_1 = \alpha_2 = 1$, *TN* x *TN* matings occur with frequency $\frac{x_1^2}{x_1 + x_2}$, *TN* x *Tn* and *Tn* x *TN* both with frequency $\frac{x_1x_2}{x_1+x_2}$, and *Tn* x *Tn* with frequency $\frac{x_2^2}{x_1+x_2}$, following Table 8.2) multiplied by the probability of producing a *t* offspring from a *T* x *T* mating, 1 - b_3. Thus, the actual rate of *T* to *t* mutation can be viewed as $\left(\frac{x_1^2+2x_1x_2+x_2^2}{x_1+x_2}\right)(1-b_3)=(x_1+x_2)(1-b_3)$, which is not affected by the **N** phenotype. Rowthorn's model predicts that, regardless of the strength of selection in favour of the 'religious predisposition' allele, and even with high defection from religious to non-religious sects, the religiosity allele will eventually fix if fertility is higher in the religious groups and the switching rates follow the inequalities listed above (Table 1, Rowthorn 2011). With cultural mutation ($b_0 > 0$, $b_3 < 1$), as well as the conditions outlined above ($\alpha_1 = \alpha_2 = 1$, $c_0 = 0$, $c_3 = 1$, $c_1 = c_2 = 0.5$, σ_1, $\sigma_2 > 0$, $\sigma_1 \neq \sigma_2$), there are two potential equilibrium points, one on the *TN-tN* edge and one on the *Tn-tn* edge, and which of these equilibria is approached depends on the relationship between the selection parameters. If $\sigma_1 > \sigma_2 > 0$, such that fertility is higher in religious groups (*T* is favoured over *t*) and those individuals with the religiosity allele are more likely to become religious (*TN* is favoured over *Tn*), analysis of this model reaches the same conclusions as Rowthorn (2011): the genetically transmitted religiosity allele approaches fixation and the culturally transmitted religious belief approaches an equilibrium determined by the transmission parameters b_0 and b_3. In the tetrahedron, there is a single stable equilibrium on the edge between the *TN* (*r, R*) vertex and the *tN* (*n, R*) vertex, corresponding to fixation of the religiosity allele and persistence of both cultural states (religious belief and non-belief), as observed by Rowthorn (2011). The rate of cultural mutation (b_0 and b_3) determines the ratio of believers to non-believers at equilibrium. Given these assumptions, however, the result of this model is similar to Rowthorn's but does not rely on the religiosity trait conferring a predisposition to religion since the genetic trait here does not impose directionally biased mutation of the cultural trait according to phenotype-specific switching rates. Instead, the genetic trait is much less specific, producing a differential selective advantage to one cultural trait over another. Indeed, if conversion occurs between the cultural states of religious belief and non-belief, then continued presence of both belief and non-belief is inevitable because neither state can reach stable fixation. Rowthorn presents an interesting model to explain the persistence of both religious belief and non-belief in humans as an alternative to an evolutionary 'spandrel' theory (Gould and Lewontin 1979). This model gives similar results without the constraint that religious predisposition is genetic, as long as cultural mutation is possible and there is a fitness advantage to the cultural trait in question.

However, Rowthorn (2011) makes a series of important assumptions that may affect the outcomes of his model. The most striking of these is complete assortment among members of religious (and non-religious) groups. Rowthorn further assumes that religious individuals, regardless of their genetic background, demonstrate a certain level of increased fertility. This regime of assorting and selection in the model, namely $\alpha_1 = \alpha_2 = 1$ and $\sigma_1 = \sigma_2 > 0$, results in a selectively neutral line of possible polymorphisms connecting the *TN*-*tN* edge to the *Tn*-*tn* edge. The exact polymorphism approached depends on the starting conditions.

Many religions have high rates of endogamy, as noted by Rowthorn, but religious groups are unlikely to have *perfect* endogamy and some mixing is inevitable (Heaton 1990). Relaxing Rowthorn's assumption and allowing assorting to be high but not complete ($0.6 < \alpha_1, \alpha_2 < 1$, following the estimates from census data in (Heaton 1990)) enables us to take account of the important effects of mixed marriages in the evolution of religiosity. In this case, there are a number of polymorphisms dependent on the values of the assortative mating parameters, the cultural transmission of religious beliefs to children of mixed marriages, and the selection pressures. Small differences in the selection pressures, however, can lead to fixation of the genetic trait while both states of the cultural belief trait persist (Figure 8.5). Although Rowthorn makes a series of suggestions regarding possible situations in which the religiosity allele may not be driven to fixation (heterozygote advantage, convergence of religious and non-religious birth rates etc.), he does not consider the effect of relaxing his strong assumption of perfect assorting. It is shown here that stable polymorphisms are possible when there is the possibility of even a small number of mixed marriages.

Cultural evolution of large-scale conflict

Our model may also help to understand in- and out-group interactions that contribute to conflict and how conflict might be alleviated. Hinde (1997) suggests that it is the culturally driven exploitation of genetic predispositions (e.g. fear of strangers) towards self-defence that leads to modern large-scale conflicts. The spread of violent tendencies in society could be largely facilitated by horizontal transmission 'catalysed by predispositions…that leave individuals particularly receptive to propaganda messages' (Laland and Brown 2002). In terms of this model, the 'cultural mutation' parameters b_0, c_0, $1 - b_3$, and $1 - c_3$ become very important in determining the eventual frequencies of cultural traits in the population. Since horizontal transmission is not included these cultural mutations can be interpreted as representing any factor that changes the beliefs of offspring relative to those of their parents. Consider the investigation by Halperin, *et al.* (2011) of the Israeli-Palestinian conflict. They exposed Israeli Jews, Palestinian citizens of Israel, and Palestinians in the West Bank to reading material suggesting that groups were either malleable in their beliefs or, alternatively, that they were fixed and unchanging in their beliefs. All of the subject groups responded to material suggesting groups were malleable with an 'increased willingness to compromise for peace' (Halperin *et al.* 2011). This type of culture-culture interaction can also be modelled using this system. It is possible to characterise one cultural dichotomy as being willingness to compromise for peace (*T*/*t*), and the other as a cultural modifier, namely an individual's belief in the malleability of groups (*N*/*n*). Individuals who place a high value on compromise might be more likely to partner with other compromisers, and, likewise, those unwilling to compromise for peace might preferentially associate with those who are also uncompromising. This entails assortative mating (or, more likely, assortative meeting, as in (Eshel and Cavalli-Sforza 1982)) based on the state of an individual's **T** trait.

Although the selection acting on such complex cultural traits is difficult to characterise, it is possible to make some simplifying assumptions. Lehmann and Feldman (2008) describe a model of 'belligerence and bravery,' two conflict-related traits. Belligerence increases the likelihood of aggression and bravery increases the likelihood of victory in the conflicts initiated by acts of aggression. The selection pressures acting on those individuals who engage in war-like behaviours are complex. On the one hand, they may have a shorter lifespan than their more peaceful counterparts, but the increased gain of fitness-enhancing resources may balance this loss. However, Lehmann and Feldman's model is probably most relevant to tribal warfare where space and access to resources and mates could be important factors in interactions with out-groups. In many modern conflicts this may no longer be the case, because the motivations and goals of large-scale industrial societal conflicts are far from fitness maximisation of the individuals who actually fight (Hinde 1987) and depend on factors at the level of the whole society (Hinde 1997). It may be sensible to assume that the evolutionary effect of reduced life expectancy for present-day combatants far outweighs any benefits accrued from increased access to resources and mates in conquered land. Thus, in applying the model presented here to modern conflicts, it may be true that selection favours compromising traits (*T*) over cultural beliefs that favour war (*t*). However, the societal pressures (e.g. manipulative media or 'mobilising and abusive leaders' (Laland and Brown 2002)) may cause the offspring of 'compromisers' to change beliefs (or actions), thus maintaining war-like phenotypes.

Such a model applied to modern warfare, therefore, is analogous to Case 4 described above with $\sigma_1 > \sigma_2 > 0$, α_1, $\alpha_2 > 0$, and $0 < b_i$, $c_i < 1$, where it is clear that, from a system initially containing all cultural traits (*TN, Tn, tN, tn*), an equilibrium in which one phenotype fixes is impossible and there is just one polymorphic equilibrium, which is critically dependent on the mutation parameters and the level of assortative mating. The model raises an interesting possibility: to the extent that a belief in group malleability is correlated with a belief in individual malleability, it may be the case that individuals lacking belief in the ability of groups (and hence individuals) to change (*n*) might choose to associate with others that share their beliefs about compromising (**T**), while those who do believe in group and individual malleability (*N*) might not preferentially partner with others that already share their beliefs, corresponding to a high value for α_2 and a low value for α_1. This could in turn lead to a population-level increase in the willingness to compromise for peace over populations in which believers in malleability also choose to assort preferentially, provided that the relative ability of *T* individuals to spread their beliefs to the next generation in mixed marriages is high enough.

Cultural evolution of sex ratio

Our model can also be applied to the cultural evolution of sex ratio bias. In China, over the past thirty years decreasing total fertility has been correlated with increasing male bias in sex ratio at birth, leading to an increasing excess of males, which has the potential for dramatic societal ramifications (Lipatov *et al.* 2011; Tuljapurkar and Feldman 1995; Li *et al.* 2000) as well as consequences for the primary sex ratio (Kumm and Feldman 1996; Kumm *et al.* 1994). In addition to the ethical concerns about sex-selective abortion and infanticide, marriage prospects for males, especially poor rural males, continue to deteriorate as the children born after the institution of China's family planning policies reach marrying age. In applying this model, it is possible to consider **T** to be a son preference trait and **N** to be a cultural modifier of this trait. An individual with *T* exhibits son preference, and an individual with *t* has no preference. The *N* and *n* states might modulate the degree to which individuals will take their partner's son preference into account when choosing a mate (i.e. assortative mating based on son preference) and the fitness benefit or cost conferred upon those who exhibit son preference (i.e. selection). It is not unrealistic to assume that an individual might not demonstrate exactly the same cultural beliefs (*T* or *t*) as his or her parents in this context; two parents with the same state might produce an offspring with the other state. As shown in Case 4, when this kind of cultural mutation is permitted, the equilibrium always has all four types present, and the location of this polymorphism depends on the exact parameter values. For example, in a scenario in which people are more likely to marry an individual who shares their cultural beliefs

(α_1, $\alpha_2 > 0$), then sons are less likely to find a mate than daughters and fitness is decreased for those that practice son preference (σ_1, $\sigma_2 < 0$). This would produce an equilibrium with more individuals exhibiting no son preference (Figure 8.2d), and it is possible to test the relative importance of selection, assortative mating, and cultural transmission in determining the equilibrium frequency of son preference. An alternative framework would have the *N*/*n* dichotomy determine a preference for virilocal marriage or no such preference. There is some evidence that virilocal marriage is correlated with an increase in the likelihood of sex selection of a foetus (Li *et al.* 2001), which is the behavioural expression of son preference.

This model of cultural evolution provides a framework for investigating the evolution of a diverse set of interacting human behaviours. It can explore cases of cultural niche construction in which one cultural trait alters the selective environment of another cultural trait, gene-culture coevolution in which a cultural trait changes selection pressures on a genetic trait, and situations in which a genetic trait influences the selection pressures on a cultural trait. The evolutionary dynamics depend on the balance between the parameters regulating cultural transmission, selection, and assortative mating. This analysis considered neutral values for each of these sets of parameters in turn and showed that polymorphisms can only persist when both assortative mating and selection are included, unless cultural mutation makes such polymorphisms inevitable. Although this chapter has suggested a few areas where the framework of the model it presents could be applicable, many more applications of this kind of cultural niche construction may be possible.

SECTION 3, CHAPTER 9

THE CULTURAL AND DEMOGRAPHIC EVOLUTION OF SON PREFERENCE AND MARRIAGE TYPE IN CONTEMPORARY CHINA

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INTRODUCTION

Niche construction is an evolutionary process whereby individuals alter their own ecological niche and so can influence the course of their, and other, species' evolution (Odling-Smee *et al.* 2003). The importance of this process in directing evolution has been discussed with respect to "ecosystem engineers" such as birds building nests or earthworms aerating the soil in which they live (Jones *et al.* 1994). An interesting, and hitherto solely human, extension of this idea is that of "cultural niche construction" (Laland *et al.* 2001). The ubiquitous nature of human culture has led researchers to believe that cultural traits may be a potent source of environmental change that has altered the course of human evolution. There is support for this idea in both recent empirical and theoretical work (e.g., Durham 1991; Feldman and Cavalli-Sforza 1989; Tishkoff *et al.* 2007; Laland *et al.* 2010; Richerson *et al.* 2010; Chapters 7 and 8). Construction of a cultural niche has the potential to impact the lives of human populations, changing both the demography of their populations and the culture in which they develop and participate.

Some culturally transmitted traits may influence the mode and extent of transmission of other cultural traits. This may occur, for example, if the frequency of one trait in a population affects the transmission and/or acceptability of another trait. Ihara and Feldman (2004) constructed such a framework in which the level of education in a population affected the cultural transmission of belief in fertility control. In general, however, "epistasis" or interaction between different traits in their transmission may or may not be frequency dependent.

Here a model using cultural beliefs regarding sex preferences in China is used to examine the potential impact of cultural niche construction on the demographic structure of human populations. First a cultural model that tracks son preferences and marriage preferences in an epidemic-style model across generations is constructed. This model is then used to inform a demographic analysis of modern China that examines potential trajectories of the demographic evolution of the population. Finally, the use of cultural niche construction models as tools to explore how best to improve the demographic trajectories of populations affected by similar sex ratio biases is discussed. Previous models of sex-ratio bias have concentrated on one cultural trait and its spread (e.g., Jiang *et al.* 2011; Laland *et al.* 1995; Li *et al.* 2000). This model examines cultural transmission and constructs a wider cultural niche composed of socio-economic status, marriage preferences, and son preferences to understand in greater detail the circumstances in which son preference is maintained and might be modified.

Sex Ratio at Birth in China

The sex ratio at birth (SRB) is the ratio of live male births to live female births. This has been found to be about 1.05 for most large human populations (Coale 1991). In some parts of the world, the SRB can be artificially elevated, sometimes dramatically, by practices reflecting a cultural bias toward male children—for example, continuing family lineage or providing security for elderly parents. This skew in SRB has been reported in a number of countries, most notably India, Bangladesh, and China (Das Gupta *et al.* 2003) and across parts of North Africa.

A number of serious consequences result from this skewed SRB. Among these is a large excess of males in the marriage market, something that has received media attention both in China and worldwide (e.g. Branigan 2011) and is predicted to cause large demographic shifts leading to an aging population (Battacharjya *et al.* 2008; Jiang *et al.* 2011). Continued male-biased SRB will lower the birth rate due to the

‘”missing marriages” caused by a shortage of women (Attané 2006). The effects of a high number of missing females is predicted to be destabilizing, leading to social unrest, increased crime rates, and a further decrease in the status of women in society, as prostitution and human trafficking become more common (Ebenstein and Sharygin 2009; Li *et al.* 2000; Tuljapakur *et al.* 1995).

The sharp decrease in total fertility rate in China since the introduction of fertility control policies in the early 1980s, coupled with the traditional son preference, is likely to cause millions of unmarried men to grow old without an economic support network or social security (Das Gupta *et al.* 2010). Chinese culture traditionally favors male children, partly as a result of the patriarchal society in which family names and inherited wealth pass through the male family line (Li *et al.* 2000), partly as a result of marriage practices that leave parents in daughter-only families in a precarious economic and social condition in old age (Das Gupta 2003; Lipatov *et al.* 2011), and partly for other cultural reasons such as the participation of sons in, and the exclusion of daughters from, certain funereal rites. The interaction between cultural son preference and the fertility-control policy implemented in China since the early 1980s has led to the Chinese SRB of about 1.18 in recent surveys. This is mediated mainly by the widespread availability of cheap ultrasound technology leading to sex-selective abortion (Banister 2004; Coale and Banister 1994; Croll 2000; Li 2007; Sen 2001; Zeng *et al.* 1993), even though it is illegal to use ultrasound-B for sex selection.

Policy interventions have been suggested as a result of mathematical and simulation models of the demographic effects of son preference (Battacharjya *et al.* 2008; Ebenstein 2011; Jiang *et al.* 2011; Li *et al.* 2000). Here a model is presented that accounts for the transmission of cultural preferences for both marriage practices and son preferences while including the effects of population structure in terms of age and socio-economic status (strongly linked to urban or rural location in China). This model can give insight into possible policy interventions and the strength with which these interventions might be implemented in order to lower the SRB in China toward natural levels.

The Cultural Evolution Model

The model assumes first that there are two major sources of son preference leading to sex selection of boys at the expense of girls in China. The first is a patriarchal society in which the family name and property pass through the male line only. The second relates to social security; daughter-only families can be left without financial security in old age due, in part, to virilocal marriage practices. Both factors contribute to reduction in the perceived value of girls in the population, with patriarchal son preference weighted by the likelihood of being in a situation where it may be desirable to sex select for a boy. In this model both the marriage practice trait and the son preference trait alter the sex ratio at birth. This changes both the age and socioeconomic demographics of the population (see below). Here it is possible to imagine the cultural traits of marriage practice and son preference as niche constructing traits altering the selective environment in which the sex ratio at birth culturally evolves, in turn shaping the transmission of those cultural traits.

To model the spread of these factors in society, an individual who has a son preference is labeled as having trait Π_1 and an individual without such a preference, trait Π_0. Similarly, an individual who believes that uxorilocal marriage is shameful has cultural trait Ω_1 and one who does not has trait Ω_0. The frequencies of Π_i and Ω_i at time t are denoted by $\pi_i(t)$ and $\omega_i(t)$, respectively.

It is then possible to define the "perceived present value" (*PPV*) of a daughter as a fraction of the perceived value of a son and, generally, $0 \leq PPV \leq 1$ owing to the prevalence of son preference, though it is not mathematically bounded between 0 and 1. This is similar in concept to the *PPV* proposed by Bhattacharjya *et al.* (2008). The *PPV* and the likelihood of sex selection are strongly and inversely correlated, meaning that as *PPV* goes up, the likelihood of sex selection for a son goes down. Thus, when *PPV = 1*, males and females are equally valued and the probability of sex selection drops to 0. *PPV* is also used in this model as the probability that a couple that can have only one more child and do not yet have a son, and are therefore in the "sex-selection situation" (Li *et al.* 2000), will choose not to sex select for a son. The probability of being in the sex selection situation, in this model, is denoted as *y*.

PPV depends on the strength of the patriarchal son preference and also on the frequency of preferences concerning uxorilocal marriage, in the following manner:

$$PPV(t) = \frac{y\omega_0(t) + \pi_0(t)}{y} \quad , \qquad (9.1)$$

where y, the probability of being in the sex-selection situation and can be interpreted as some measure of the biological significance of the trait *Π₀*. Here, if *PPV* is reduced such that $PPV = 1 - \alpha$, say, it is possible to write that $y(1 - \alpha - \omega_0) = \pi_0$ where $y\alpha$ represents the increase in son preference engendered by the lower *PPV*. Here there is an assumption that when $\omega_0(t) = \pi_0(t) = 1$ (both frequencies are at their maximum values), $PPV = \frac{y+1}{y}$. This implies that the perceived value of girls may still depend to a certain extent on the probability of being in the sex-selection situation, *y*. Note also that if $PPV = 1$, equation (9.1) entails that $y\omega_1(t) = \pi_0$, so there is a balance among the frequency of son preference, the chance of being in the sex-selection situation, and preferring uxorilocal marriage.

To find an expression for $\omega_0(t+1)$, the frequency of *Ω₀* in the next generation, the model first assumes that individuals who have trait *Ω₀*, and who do not believe that uxorilocal marriage is shameful, will be equally likely to marry uxorilocally or virilocally. There is an assumed proportion, *W*, of individuals who are forced to marry uxorilocally despite having trait *Ω₁* because they are unable to afford a brideprice. In this way, *W* can be viewed as a measure of poverty in the population. Here, all uxorilocal marriages contribute to an increase in the *PPV* for girls, and even individuals who marry uxorilocally out of necessity spread the *Ω₀* trait by example. This means that the expected proportion of marriages that are uxorilocal in generation *t* is

$$\frac{\omega_0(t)}{2} + W(1-\omega_0(t)) \ , \qquad (9.2)$$

that is, half those with a neutral marriage preference plus those who consider uxorilocal marriage shameful but lack the resources to make a virilocal marriage. Vertical cultural transmission is assumed to take place before horizontal cultural transmission.

The frequency of *Ω₀* in the next generation is then given by

$$\omega_0(t+1) = \omega_0^V(t) + H_{\omega_0}\omega_1^V(t)\omega_0^V(t) , \qquad (9.3)$$

where $\omega_0^V(t)$ is the frequency of *Ω₀* at time *t* after vertical transmission and is given by $\omega_0^V(t) = V_{\omega_0}\left(\frac{\omega_0(t)}{2} + W\omega_1(t)\right)$ with V_{ω_0} the rate of vertical transmission of Ω_0.

Assuming a constant fertility rate among married couples, $\frac{\omega_0(t)}{2} + W\omega_1(t)$ is both the fraction of marriages at time t that are uxorilocal *and* the fraction of offspring at time $t+1$ who are from an uxorilocal marriage and thus are subject to vertical transmission, by example, of a neutral belief, Ω_0, about the marriage practice.

For the dynamics of π_0 the model considers (1) the probability that an individual will be in sex-selection situation y and (2) the normal sex ratio for humans in large groups, which is the ratio of the number of males born divided by the number of females born or $s_0 = \frac{m_0}{f_0}$. Using s_0 allows us to reduce the number of parameters and discuss the *SRB* in China in terms of the normal *SRB* for large human populations. Then

$$\pi_0(t+1) = V_{\pi_0}\frac{PPV(t)}{1+s_0}y + H_{\pi_0}\pi_0(t)\left(1 - \frac{PPV(t)}{1+s_0}y\right) \qquad (9.4)$$

is the fraction of girls at time $t+1$ who have trait Π_0, where H_{π_0} and V_{π_0} are the rates of horizontal transmission and vertical transmission, respectively, of Π_0. Here, $\frac{PPV(t)}{1+s_0}y$ is the probability that a girl is born to a mother in the sex-selection situation at time t. Note that if $0 \leq PPV(t) \leq 1$ and $f_0 < m_0$, given that $s_0 = 1.05$, this means that the quantity $\frac{PPV(t)}{1+s_0}y$ is typically less than one, even at the natural sex ratio. The proportion of male children born to each woman who bears children is

$$1-\frac{PPV(t)}{1+s_0}y. \qquad (9.5)$$

Hence the sex ratio at birth (SRB) in the next generation is

$$SRB(t+1)=\frac{1-\frac{PPV(t)}{1+s_0}}{\frac{PPV(t)}{1+s_0}y}. \qquad (9.6)$$

On substituting Equation (9.1) into Equation (9.4), the right-hand side becomes a function of $\pi_0(t)$ and $\omega_0(t)$. Together with Equation (9.3), this forms a pair of recursions that express $\pi_0(t+1)$ and $\omega_0(t+1)$ in terms of $\pi_0(t)$ and $\omega_0(t)$. The recursion system can be numerically iterate to equilibrium, or equilibrium can be assumed and the nonlinear simultaneous equilibrium equations solved. The stable equilibrium from this analysis can then be used to construct the equilibria for *PPV* and using Equation (9.6), for *SRB*. It is then possible to examine how *PPV* and *SRB* change with the transmission parameters H_{ω_0}, V_{ω_0}, H_{π_0}, V_{π_0} and the probability of being in sex-selection situation, y.

RESULTS

Using the equilibrium values described above, it is possible to investigate the effects of the model parameters on the eventual frequencies of the cultural traits and hence the final equilibrium values of the *SRB* and *PPV*. The parameters can be fixed at reasonable values and varied in turn. In Figures 9.1a and 9.1b, the effects of the rates of cultural spread of son and marriage preference on the equilibria, which are denoted as *PPV** and *SRB** are clear. From Figures 9.1 and 9.2 it is clear that the most dramatic differences in these equilibria values are caused by the horizontal transmission parameters (H_{π_0}, H_{ω_0}) describing both the spread of no son preference (*Π₀*) and no marriage-type preference (*Ω₀*) and the probability of being in the sex selection situation, *y*. It is these parameters that are emphasised when examining the possibility of policy interventions.

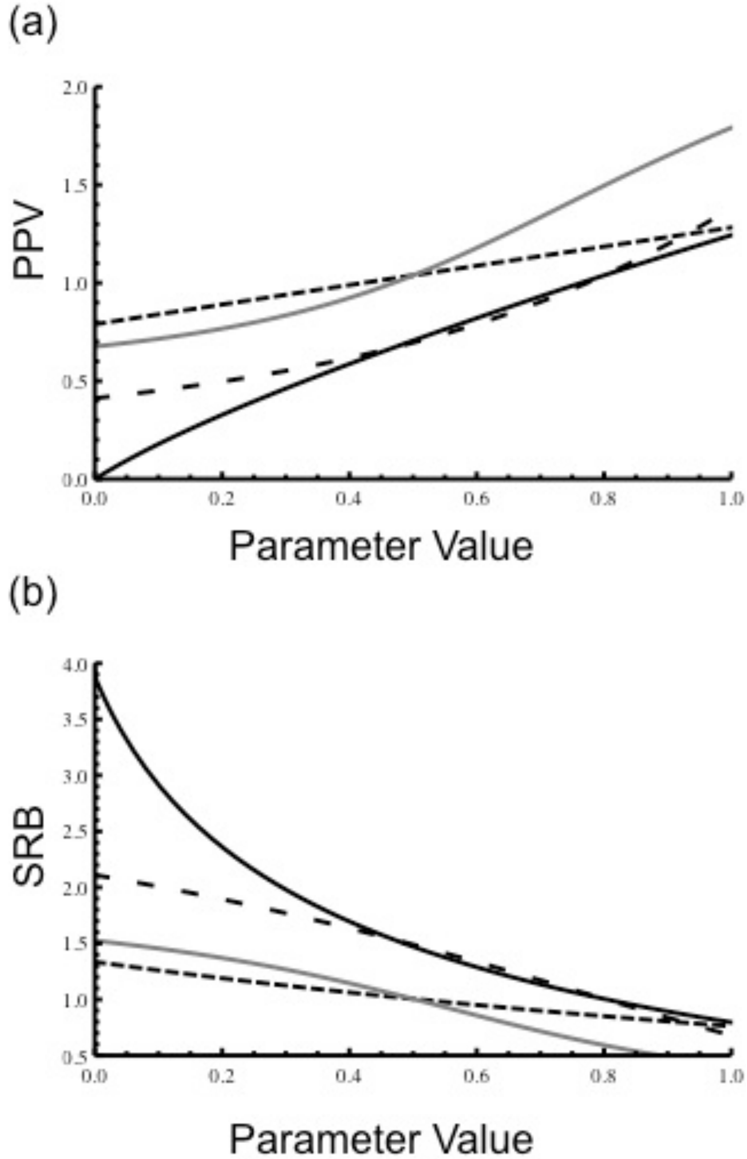

Figure 9.1: (a) The effect of V_{π_0} (long dash), V_{ω_0} (black solid), H_{π_0} (grey), H_{ω_0} (short dash) on the perceived present value of girls in the model. $s_0 = 1.05$, $y = 0.58$, $W = 0.3$, $H_{\omega_0} = H_{\pi_0} = 0.5$, $V_{\omega_0} = V_{\pi_0} = 0.8$ (b) The effect of V_{π_0} (long dash), V_{ω_0} (black solid), H_{π_0} (grey), H_{ω_0} (short dash)

on the sex ratio at birth in the model. $s_0 = 1.05$, $y = 0.58$, $W = 0.3$, $H_{\omega_0} = H_{\pi_0} = 0.5, V_{\omega_0} = V_{\pi_0} = 0.8$

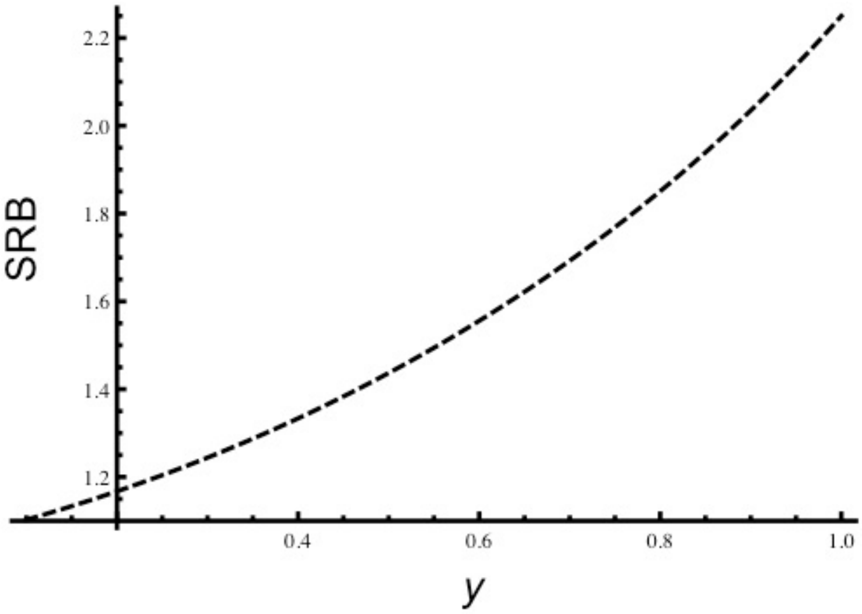

Figure 9.2. The effect of the likelihood of being in the sex selection situation, y, on the sex ratio at birth in the model. This can be thought of as the strength of the one-child policy or its enforcement. Other parameters are fixed at $s_0 = 1.05$, $W = 0.3$, $H_{\omega_0} = H_{\pi_0} = 0.3$, $V_{\omega_0} = V_{\pi_0} = 0.7$

Population Structure and Demographic Models

The previous model can be extended to include demography. To do this both age stratification (as in Li *et al.* 2000) and socio-economic stratification in the population are included. This extension allows analysis of the effects of male-biased sex ratio at birth in poor rural areas, where marriage practices may be stricter but money in shorter supply, and richer areas, where the one-child policy may be more strictly enforced, for example.

Age Structure

One consequence of the steep decline in birth rates seen in China since the introduction of the one-child policy is an increase in the average age of the population. This becomes economically problematic when the older generation is not replaced in the workforce by sufficient younger individuals. Perhaps more importantly, it raises concerns over the social welfare, health, and wellbeing of the older population and the heavy burden of this care on the young. Thus there is also considerable interest in managing the balance between old and young in the future Chinese population. This model investigates ways to track age structure through cultural evolution of fertility and marriage practices within the constraints of the one-child policy.

The three age classes represent pre-reproductive, reproductive, and post-reproductive women respectively without any specific assumptions about the exact ages at which individuals occupy these classes. Each economic class is assumed to have a Leslie matrix (Leslie 1945) that describes the dynamics of age structure of its members. The Leslie matrix for each economic class has the structure

$$\bar{n}(t+1) = \begin{pmatrix} F_1 & F_2 & F_3 \\ \sigma_1 & 0 & 0 \\ 0 & \sigma_2 & 0 \end{pmatrix} \bar{n}(t) \ ,$$

where F_a denotes the fertility rate within the age class *a,* σ_1 and σ_2 are survival probabilities for age classes 1 and 2 respectively, and $\bar{n}(t)$ is the vector of the number of individuals in each age class at time *t*.

From the cultural transmission model outlined above, the number of daughters born to each woman in the reproductive age classes is given by

$$TFR*\left(\frac{PPV(t)}{1+s_0}y\right), \tag{9.7}$$

where TFR denotes the total fertility rate of the population. Given that $F_1=F_3=0$ and F_2 is the only reproductive class, the Leslie matrix becomes

$$\bar{n}(t+1)=\begin{pmatrix} 0 & TFR*\left(\dfrac{PPV(t)}{1+s_0}y\right) & 0 \\ \sigma_1 & 0 & 0 \\ 0 & \sigma_2 & 0 \end{pmatrix}\bar{n}(t) \tag{9.8}$$

The dominant eigenvalue for the matrix in equation (9.8) is

$$\lambda_n=\sqrt{\frac{\sigma_1 TFR(1+y(PPV^*-1))}{1+s_0}} \tag{9.9}$$

and the corresponding eigenvector is

$$\bar{v}=\left(\frac{TFR-TFRy+PPV^*TFRy}{\sigma_2+s_0\sigma_2},\frac{\sqrt{\dfrac{\sigma_1 TFR(1+y(PPV^*-1))}{1+s_0}}}{\sigma_2},1\right). \tag{9.10}$$

To find a stable age structure for this population, the cultural traits are assumed to have reached equilibrium and that PPV^* can be used from the cultural model above. For the stable age distribution, The elements of the eigenvector (Equation 9.10) are divided by their sum to obtain the stable proportion of the female population in each age class.

Horizontal Transmission and Age Structure

Using the stable age distribution and the cultural equilibrium of *PPV* (PPV^*), it is possible to investigate the effects of horizontal transmission of patriarchal son preference and beliefs about marriage practices for fixed values of vertical transmission, enforcement strength of the one-child policy, and survival rates of the age classes. Figure 9.3a shows the effect of horizontal transmission of marriage preference, and Figure 9.3b shows the effect of horizontal transmission of son preference for a fixed value of horizontal transmission of marriage type preference. Figures 9.3c and 9.3d show the same for vertical transmission, on the age structure of the population. The ideal age structure for a population is a balance between class 2 and the other two classes that is economically sufficient to maintain the dependents. A high dependency ratio is generally of concern as societies struggle to maintain social security of an increasingly aged population unable to work to sustain themselves. It is clear from Figures 9.4 and 9.5 that this ideal demography becomes possible for some higher values of horizontal or vertical transmission in some cases.

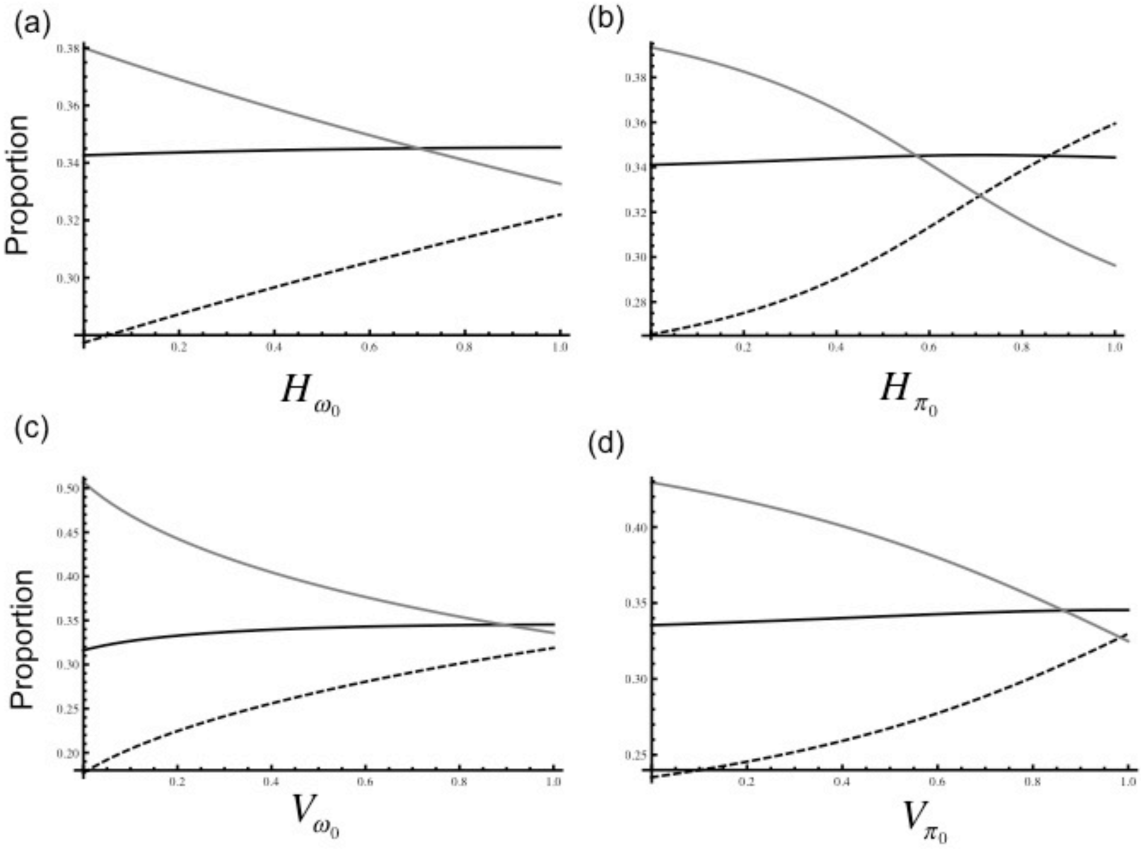

Figure 9.3: The effect of (a) H_{ω_0} (b) H_{π_0} (c) V_{ω_0} and (d) V_{π_0} on the age structure of the population, Age class 1 (dash), age class 2 (black) and age class 3 (grey). *TFR* = 1.5, σ_1= 0.98, σ_2= 0.88, $s_0 = 1.05$, $y = 0.58$, $W = 0.3$, $H_{\omega_0} = H_{\pi_0} = 0.5, V_{\omega_0} = V_{\pi_0} = 0.8$. Estimates for σ values are from mortality figures generated from W.H.O. health statistics and health information systems.

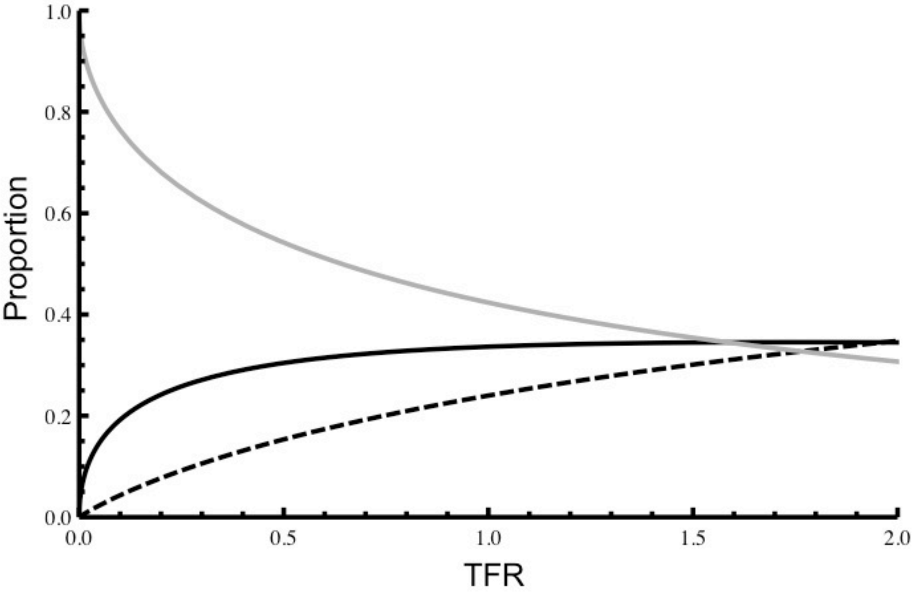

Figure 9.4. The effect of *TFR* on the age structure of the population, Age class 1 (dash), age class 2 (black) and age class 3 (grey). s_0= 1.05, y = 0.58, W=0.3, $H_{\omega_0} = H_{\pi_0} = 0.5$, $V_{\omega_0} = V_{\pi_0} = 0.8$, σ_1= 0.98, σ_2= 0.88.

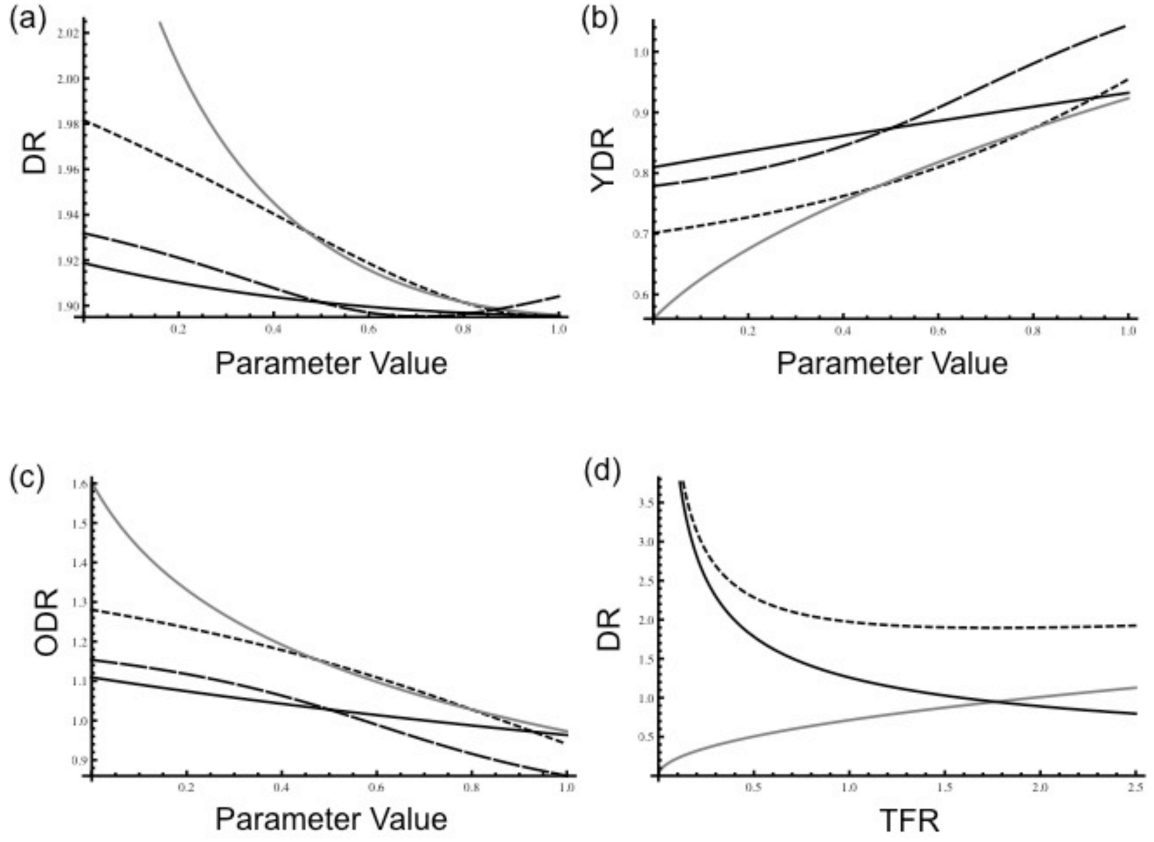

Figure 9.5. (a) The full dependency ratio (DR) for the age class system, (b) the youth dependency ratio (YDR) and (c) the old age dependency ratio (ODR), changing with parameters H_{ω_0} (black), H_{π_0}(long dash), V_{ω_0}(grey) and V_{π_0}(short dash). *TFR* = 1.5, σ_1= 0.98, σ_2= 0.88, $s_0 = 1.05$ $y = 0.58$, $W = 0.3$, $H_{\omega_0} = H_{\pi_0} = 0.5, V_{\omega_0} = V_{\pi_0} = 0.8$.

Socio-economic Structure

The SRB might change if living standards and opportunities afforded to the rural poor in China are improved. This is of particular interest given that individuals in many rural areas are poorer and often subject to less stringent enforcement of the one-child policy than their urban counterparts. It is also true that the recent economic boom in China has meant that migration of one or more family members to cities from rural areas in order to increase income is a major feature of many rural Chinese households. To examine these effects, a social-mobility matrix is introduced that describes the proportion of the population in each of three socio-economic classes (rural poor, urban poor, and urban rich) and the movement from one class to another over successive generations.

For simplicity, it is assumed that people can move only to a higher social class and must do so incrementally. These assumptions can later be relaxed or removed if necessary. The social-mobility matrix can then be written as

$$\bar{m}(t+1) = \begin{pmatrix} S_1 + 1 - \delta_1 & 0 & 0 \\ \delta_1 & S_2 + 1 - \delta_2 & 0 \\ 0 & \delta_2 & S_3 + 1 \end{pmatrix} \bar{m}(t), \qquad (9.11)$$

where $\bar{m}(t)$ is the vector containing the number of individuals in each socio-economic sector at time t and S_j is a population change parameter in the jth socio-economic class, incorporating both birth and death rates. Negative values of S_j indicate higher death than birth rates, and positive values indicate higher birth than death rates. Finally, δ_j denotes the likelihood of moving from the jth socio-economic sector to the $j+1$th sector.

Just as the simple cultural model generated the birth rate for use in the age-class model, it is possible to use the overall birth rate from the age-class model in each separate socio-economic sector to inform the socio-economic model. The dominant eigenvalue for the matrix in equation (9.11) is

$$\lambda_m = S_1 + 1 - \delta_1 \qquad (9.12)$$

with corresponding eigenvector

$$\bar{w} = \left(\frac{(\delta_1 - \delta_2 - S_1 + S_2)(\delta_1 - S_1 + S_3)}{\delta_1 \delta_2}, -\frac{(\delta_1 - S_1 + S_3)}{\delta_2}, 1 \right) \tag{9.13}$$

This model can be extended by including the wealth parameter, W, from the original cultural transmission model. W describes the proportion of the population that is *unable* to afford a bride price (see equation 9.2). As such, W is perhaps better described as a measure of poverty within a socio-economic sector. Values of δ_j depend on the level of poverty in the jth sector in the following way:

$$\delta_j = (1 - W_j) d_j \tag{9.14}$$

where d_j is a constant rate of social mobility, a feature of the jth class (this could be interpreted as ease of forming useful social networks, for example), and W_j is a measure of the level of poverty (as measured by the inability to afford a bride price) in the jth sector.

The model can then be made more realistic by allowing the individuals that move from, say, sector i to sector k to bring their cultural beliefs with them into their new surroundings for one generation. This is done by adjusting the values of S_j to account for the presence of a proportion of the population carrying ideas formed in their former socio-economic group. This involves including an equation for the *PPV* in each social sector. It is then possible to re-label *PPV* as *PPV*$_j$, π_0 as π_{0j}, ω_0 as ω_{0j} and the learning parameters H_{ω_0}, H_{π_0}, V_{ω_0} and V_{π_0} become $H^j_{\omega_0}$, $H^j_{\pi_0}$, $V^j_{\omega_0}$ and $V^j_{\pi_0}$ respectively, where $j = \{1, 2, 3\}$ represents the socio-economic sector. Using equation (9.1), a system of equations is obtained, one equation representing the *PPV* in each social sector;

$$PPV_1 = \frac{y_1\omega_{01} + \pi_{01}}{y_1} \tag{9.15}$$

$$PPV_2 = \frac{y_2(\tau_1\omega_{01} + (1-\tau_1)\omega_{02}) + (\tau_1\pi_{01} + (1-\tau_1)\pi_{02})}{y_2} \tag{9.16}$$

$$PPV_3 = \frac{y_3(\tau_2\omega_{02} + (1-\tau_2)\omega_{03}) + (\tau_2\pi_{02} + (1-\tau_2)\pi_{03})}{y_3} \tag{9.17}$$

where $\tau_1 = \frac{\delta_1\bar{m}_1}{\bar{m}_2}$ and $\tau_2 = \frac{\delta_2\bar{m}_2}{\bar{m}_3}$, with $\bar{m}_j$ representing the normalized elements of the stable socio-economic distribution in the *j*th sector obtained from the eigenvectors corresponding to (9.13). Using these equations, it is possible to gain a better understanding of the effect of wealth, social mobility, and one-child policy enforcement in different socio-economic sectors on the *SRB* within that sector and the changes that this makes in other social sectors. To this end, one simplifying assumption is made to prevent the problem from becoming mathematically intractable: it is assumed that the equilibrium values within each socio-economic sector are reached sequentially. In this formulation, the *PPV*s in all sectors of society are functions of the parameters in all other sectors. This is an interesting and useful exercise as it is possible that increasing, for example, the horizontal transmission of ideas in the lowest socio-economic sector and allowing an increase in social mobility might reduce the need for direct intervention in higher socio-economic sectors (Figure 9.6). This possibility may reduce the overall cost of effective intervention.

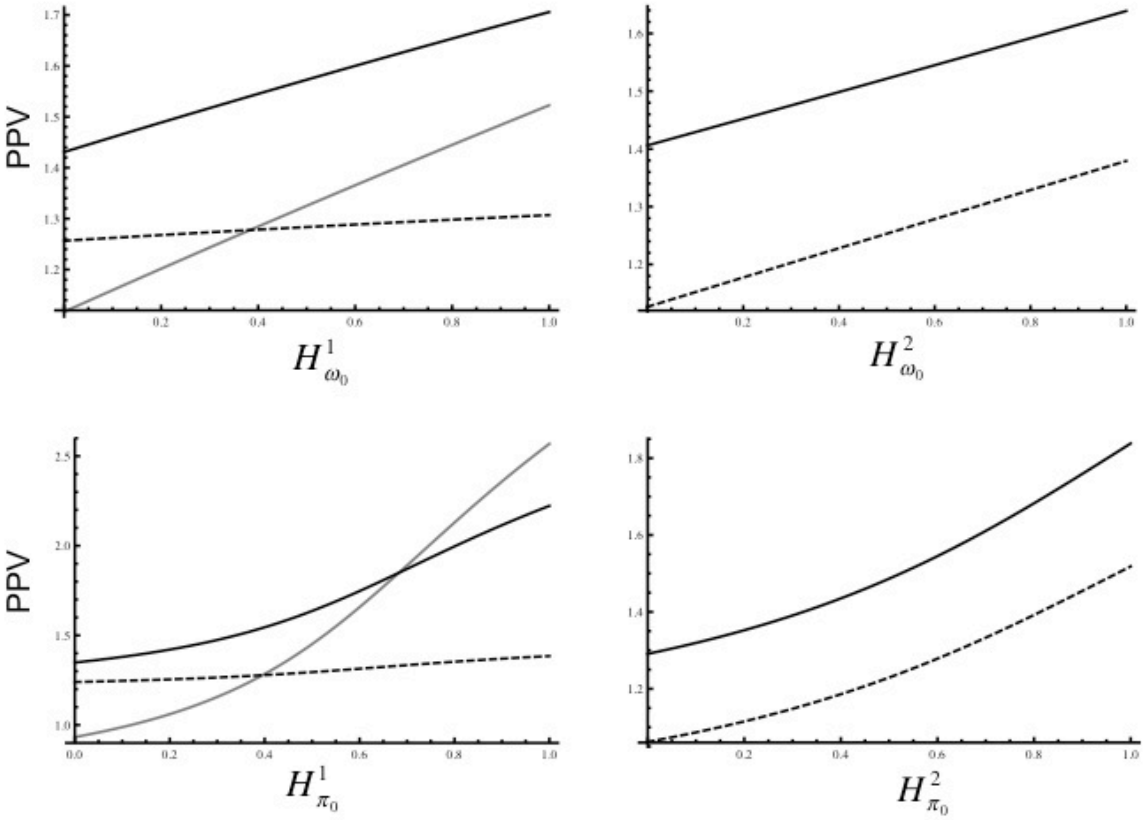

Figure 9.6. Change in *PPV* in socio-economic sectors 1 (grey), 2 (black) and 3 (dash) with changes in the horizontal transmission of (a) neutral marriage preferences in sector 1, (b) neutral marriage preferences in sector 2, (c) no son preference in sector 1 and (d) no son preference in sector 2. Other parameters are: $s_0 = 1.05$, $y_1=0.4$, $y_2=0.58$, $y_3=0.8$, $W_1=0.7$, $W_2=0.4$, $W_3=0.2$, $H^1_{\omega_0} = H^1_{\pi_0} = 0.4$, $V^1_{\pi_0} = V^1_{\omega_0} = 0.8$, $V^2_{\pi_0} = V^2_{\omega_0} = 0.5$, $H^2_{\omega_0} = H^2_{\pi_0} = 0.6$, $V^3_{\pi_0} = V^3_{\omega_0} = 0.3$, $H^3_{\omega_0} = H^3_{\pi_0} = 0.8$, $d_1 = 0.2$, $d_2 = 0.3$

DISCUSSION

A male-biased skew in the sex ratio at birth is a growing problem across Asia and North Africa (Croll 2000; Das Gupta *et al.* 2003). The human cost is estimated to be between 60 million (Coale 1991) and 100 million (Sen 1990) missing women worldwide, with many more societal problems developing as the sex ratio worsens (Jiang *et al.* 2011; Li *et al.* 2000; Tuljapakur *et al.* 1995). Although investigations of the economic factors that maintain son preference are useful, they must be combined with an understanding of the cultural niche that maintains and spreads sex preferences, including any cultural norms that may affect the perceived value of women in society and in turn contribute to the demographic make-up of the population as a whole. To the extent that a cultural trait maintains tight control on the structure of the population, it can also control aspects of mate choice feeding back onto the genetic evolution of those occupying that cultural niche. In this case, the feedback can change the biological SRB, raising it or lowering it under different conditions (Laland *et al.* 1995).

This model concentrates on two important causes of son preference in China: (1) the cultural spread of a belief that sons are more valuable than daughters and (2) the spread of beliefs about marriage practices. It includes both cultural and demographic factors, allowing examination of the impact of the bias in *SRB* on the age structure and dependency ratios, which are of growing concern in China. High dependency ratios lead to economic and psychological strain on all sectors of society and can drive an increase in poverty both in the dependent sectors and in the sector on which they depend. The age structure is therefore an important factor in any analysis of the social impacts of son preference. This chapter shows that an increase in the transmission of neutral marriage beliefs (Ω_0) and absence of son preference (Π_0) through any channels will have a positive impact, raising the *PPV* and lowering the *SRB* as well as altering dependency ratios in the system. These findings agree largely with those of Jiang *et al.* (2011), who also showed that an increase in the effectiveness of policy interventions aimed at spreading neutral beliefs about son preference decreased the sex ratio and improved the outlook for dependency ratios, as compared with scenarios that did not involve such intervention. However, it is also of practical importance to know how much change can be exacted, and how this change will manifest, in order to allow successful intervention in economically restricted circumstances.

Possible Policy Interventions

Our analysis implies that models examining human cultural niches in detail can be useful as tools to predict how best to change and improve the lives of those who have created or inherited those niches. Certain parameter values in the model are more likely than others to be more easily changed through cultural intervention by the authorities. This means that when considering a possible intervention, there is a trade off between the parameters that are easiest to change and what impact that change will have on the values of the *PPV* and the *SRB*. From Figures 1a and 1b it is clear that horizontal transmission of son preference (H_{π_0}) and vertical transmission of marriage practices (V_{ω_0}) have the biggest effects on the equilibrium value of the *SRB*. Horizontal (and to an extent oblique) transmission has the added advantage of being the most obvious form of information transfer available to policy makers. It is possible to increase the level of horizontal transmission, for example, by increasing expenditure on media advocating a pro-daughter message or raising awareness of the problem more generally. The model can be used to provide information about how much money and how much advertising would be needed to increase awareness of the *SRB* problem sufficiently to reduce *SRB*.

To start, it is important to note that horizontal transmission rates are bounded such that $0 \leq H \leq 1$. Using the example of transmission through access to education, it is possible to introduce another variable describing the proportion of the population with access to school age education. This acts as a new upper limit on the strength of horizontal transmission. For example, suppose $0 \leq H \leq E$, where E is the proportion of the population with access to education or television. The assumption can then be made that the spread of information or cultural ideas follows a linear pattern dependent on the absolute rate of information transfer, a property of the teaching methods employed, the number of hours of exposure to, for example, a pro-daughter message and capped at the proportion of the population with access to the message (i.e. advertising or education reform can at most change the minds of all individuals who are exposed to it).

Using this logic to construct a bound for the effect of horizontal transmission per hour, for example,

$$H = rxE \tag{9.18}$$

where x is the number of hours per day dedicated to changing Π and Ω cultural beliefs, E is the proportion of the population that has access or exposure to the education campaigns, and r is the absolute rate of information transfer. Using (9.18) it is possible to plot the value of H for changing values of x, E, and r, the results of which are shown in Figure 9.7. Equation (9.18) can easily be modified to account for different learning processes associated with different teaching methods or types of information transfer with a different (per hour) rate of learning for each type.

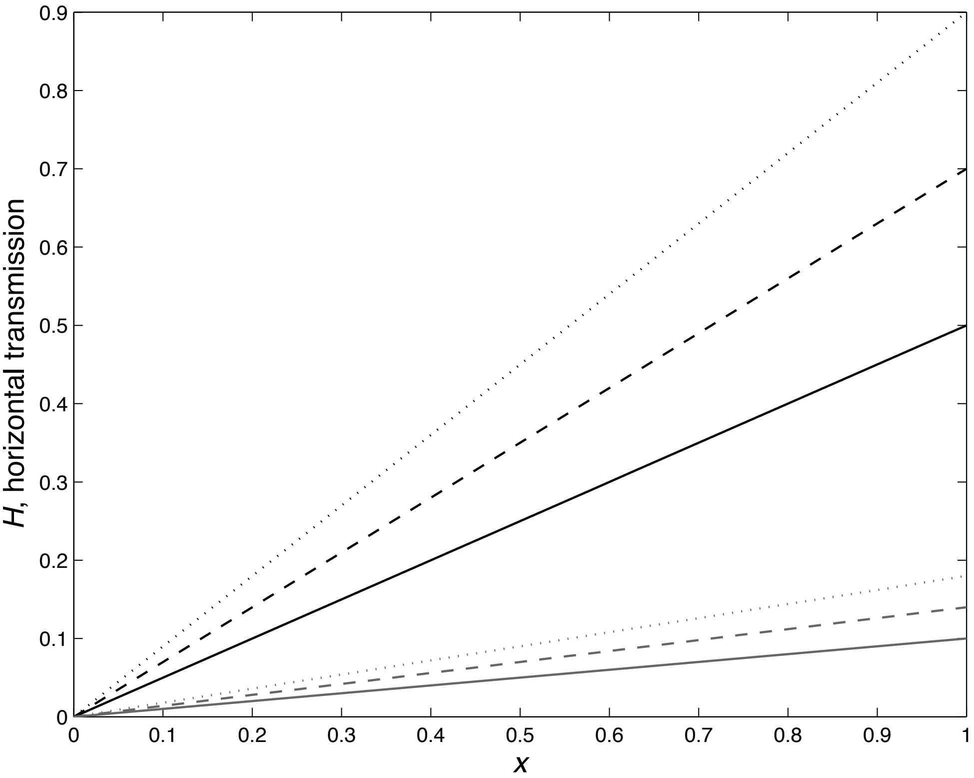

Figure 9.7. The values of H from equation 9.18 generated by hours of advertising, x, and access to education or mass media, E=0.5 (solid), E=0.7 (dashed), E=0.9 (dotted), values for two values of r, $r=0.2$ (grey lines) and $r=1$(black lines).

Using this extension, it is simple multiplication to assess the monetary cost of proposed media intervention; the model can allow policy makers to determine the value of H for which they can expect a decrease in *SRB*, or an eventual return to a normal *SRB*. The corresponding value of x is here labelled as $\hat{x}$. Introducing a cost, c, to the production and distribution of advertising per hour, the total cost, c_{total} is given by $c_{total} = c\hat{x}$. For school-age education, the limiting factor would be children's (especially girls') access to education. In this case the parameter r, describing the absolute learning rate per unit time, could potentially be quite high. An alternative involves mass media campaigns, in which case the limiting factor, E, would represent the proportion of the population with access to mass media. Although this is potentially a cheaper method of information transfer, the fidelity of transmission is also potentially lower.

Age Structure and Socio-economic Model

The age-structure model shows that the transmission parameters may change, and in some cases, even reverse, current demographic trends, via the horizontal transmission of no son preference (H_{π_0}), which is capable of driving the proportion of the female population in age class 1 above the proportion in age classes 2 or 3 (Figure 9.3b). Many of the problems associated with sex-ratio bias, combined with fertility controls, are problems of over-dependence on the shrinking working-age sector of society. To examine possible solutions to these problems, the full dependency ratio (DR), the old-age dependency ratio (ODR), and the youth dependency ratio (YDR) were calculated for the cultural demographic model presented above. Figure 9.5 shows the impact of the transmission parameters (H_{π_0} , H_{ω_0} , V_{π_0} and V_{ω_0}) on these ratios. As the transmission of pro-daughter cultural traits increases, both the DR (Figure 9.5a) and the ODR (Figure 9.5c) decrease. The increase in YDR with transmission parameters (Figure 9.5b) reflects an increase in the birth rate of daughters.

Total Fertility Rates

Another important avenue of investigation concerns the effects that a change in total fertility rate (*TFR*) would have on the *PPV*, *SRB,* and demographic structure (see also Jiang *et al.* 2011). To investigate these effects, all other parameters were fixed and TFR was varied between 0 and 2. Here *TFR* is modelled as a constant but its interaction with other factors like age structure may be interesting areas for further development. Of particular concern is the possible changes that occur between *TFR* =

1.5 and *TFR* = 2. This change, together with a lowering of y, the probability of being in the sex selection situation, would represent a relaxation of fertility control policies in effect in China today. As with the transmission parameters, a change in TFR and y seems capable of changing current demographic trends (Figure 9.4) and lowering the full-dependency ratio in the system (Figure 9.8). As y decreases, the *SRB* also decreases, eventually returning to natural levels ($s_0 = 1.05$) (Figure 9.2).

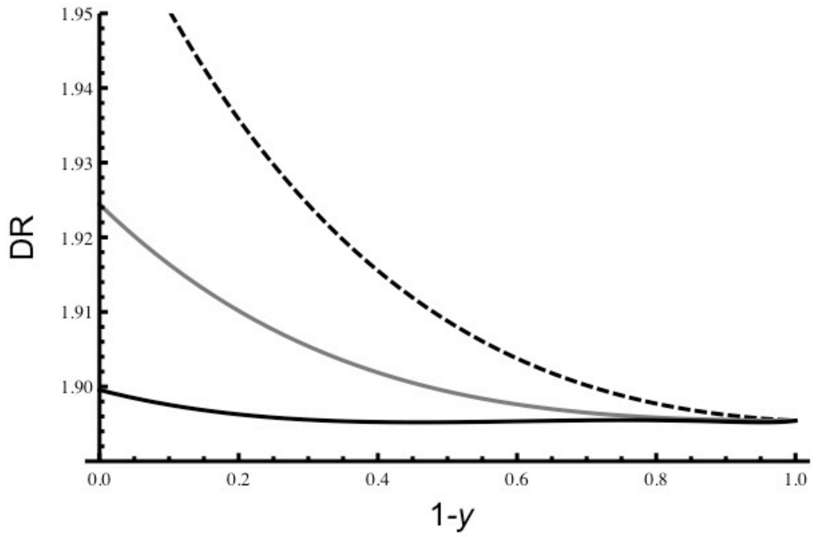

Figure 9.8. The full dependency ratio for $V_{\pi_0} = 0.4$ (dashed), $V_{\pi_0} = 0.6$ (grey) and $V_{\pi_0} = 0.8$ (black), changing with 1-y. TFR = 1.5, σ_1= 0.98, σ_2= 0.88, $s_0 = 1.05$ $y = 0.58$, $W = 0.3$, $V_{\omega_0} = 0.8, H_{\pi_0} = H_{\omega_0} = 0.5$

The kinds of cultural interventions described above could complement more economic interventions such as the “Care for Girls” program, mandated to improve survival and development prospects for girls, and other programs, such as those proposed by Jiang *et al.* (2011). Care for Girls works by improving access to education for girls from daughter-only families and by providing these families with a monetary allowance designed to lessen the impact of poverty in old age. Programs like these could interact with other more culturally focused interventions by increasing access to education and thus peer-to-peer contact, both of which could lead to a rise in horizontal transmission and a decrease in *SRB*, according to the model. More financial support for daughter-only families might also give parents the freedom to allow or even encourage uxorilocal marriage, increasing the transmission parameter V_{ω_0} . The model presented here suggests that an intervention program such as "a new notion of marriage and childbearing into ten thousand families," which was integrated with the Care for Girls program in the early 2000s (Zheng 2007), could be effective in increasing *PPV* and ultimately lowering *SRB*.

SECTION 4:

GENERAL DISCUSSION

SECTION 4, CHAPTER 10

DISCUSSION: SOCIAL LEARNING, CULTURE AND SOCIETY

Material from this chapter has been published as:

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Human culture is arguably the most complex phenomenon known to science (Plotkin 2010). To fully understand culture we must understand the selection pressures that shaped brains capable of creating it, as well as the properties of cultural transmission and the feedback between biological and cultural evolution that maintains it.

Here I would like to draw out three important themes that underlie the research presented in this thesis, which help to elucidate this complex system in a number of ways. The first is the importance of population structure, including spatial structure and assortative mating interactions, in models of the evolution of social learning and cultural evolution. This is most obvious in Chapters 2 and 7, which are explicitly spatial simulation models, both with non-spatial ancestors showing qualitatively different results. However, the effects of the restricted mixing that we see in spatial models are also present, to an extent, in the models presented in Chapters 8 and 9, with the former investigating the effects of assortative mating on a cultural niche construction model and the latter investigating the effects of social stratification on sex-ratio bias in modern China.

The second theme, that runs especially through Chapters 3, 4, 5 and 6, is that the fidelity of information transmission, and the strategies through which individuals learn, have a profound affect on the characteristics of the cultures that can emerge. Such effects include impacts on cultural diversity, longevity of traits, evenness of trait distribution and the probability of generating complex cognitive capacities like the ability for cumulative culture.

Third, with respect to the chapters contained in Section 3, three chapters dealing exclusively with human culture, I argue that the complexities peculiar to modelling human cultural systems require models that are general to allow straightforward and valid comparisons, but also require tailored models to accommodate very specific policy-based approaches. Mathematical approaches can have different functions, domains and levels of analysis, and pluralism of approach is necessary for a complete understanding (Levins 1966).

The Importance of Spatial and Population Structure

As described in the introduction, Rogers (1988) proposed a simple model of the evolution of social learning that captured what researchers (e.g. Boyd and Richerson 1985) had suggested was the root of the adaptiveness of social learning and particularly of human culture: that social learning allowed individuals to avoid the fitness costs associated with individual learning while still accumulating a useful body of knowledge. Rogers' model focused on a hypothetical species living in one of two possible environments and expressing one of two possible behavioural traits, with each trait being adaptive in one environmental state, and with the environment switching from one state to the other with a fixed probability. In the model there were also two learning genotypes: *individual learners* and *social learners*. *Individual learners* gained information directly from the environment at some cost to their fitness while the *social learners* copied a randomly chosen individual at no cost. Rogers found that social learning failed to increase the fitness of the population above that expected of a population of asocial learners (Figure 1.1), a counter-intuitive finding that was labelled 'Rogers' paradox of non-adaptive culture'.

As discussed in Chapter 1, Boyd and Richerson (1995) examined Rogers' paradox and concluded that it would arise in any evolutionary game where social and asocial learners played against each other and the value of the learned information remained frequency independent. This confirmed that the problem was general. Enquist *et al.* (2007) found that *critical social learners* who copy first and only rely on asocial learning when copying fails and *conditional social learners* who rely on social learning only when asocial learning fails both resolved Rogers' paradox by increasing the mean fitness of the population above that expected of a population of asocial learners and pure random social learners.

Chapter 2 presented an extension of Rogers' analysis where the original 1988 model was applied to a grid of individuals who could interact with their eight closest neighbours (the Moore neighbourhood) only, with periodic boundary conditions. This simple extension offered a further solution to the original paradox, while drawing attention to another counter-intuitive finding: that the proportion of pure social learners could actually continue to increase in the population even while driving fitness below that of the original asocial learner population.

Conditions under which the *conditional social learning* strategy is favoured over the *critical social learning* strategy were also seen in Chapter 2, when the environment was spatially variable. *Conditional social learning* could invade when asocial learning was unreliable, the environment was highly stable, and when the cost of asocial learning was low. Under these conditions, *conditional social learners* had an advantage over asocial learners when asocial learning failed, and when social learning was useful (e.g. in stable environments). However, the payoff was relatively small, and so only had an effect when learning costs were generally low, hence the counter-intuitive result that a social learning strategy could invade a population of asocial learners when the cost of asocial learning was low. This is also the region where *conditional social learners* outperform *critical social learners*. The latter cannot become established in stable environments because it is difficult for the benefits of social learning to outweigh the low costs of asocial learning.

The spatial aspect of this model also showed some circumstances in which pure social learning out-competed not only individual learning but both *critical* and *conditional social learning* strategies too. The root of this surprising finding was that the social learning genotype was buffered from the invasion of more fit asocial learners in social learning spatial clusters (Figure 2.2a), with a cluster here defined as a contiguous group of individuals who have at least one immediate neighbour sharing their particular strategy (Langer *et al.* 2008))

The clustering effect in social learning models is a subtle one. Social learners are essentially parasites, gleaning useful information from asocial learners and suffering little or no cost for doing so, if the information is correct. In the context of this model, this free information is recycled again and again, becoming out-dated as the environment changes. This means that as social learners cluster together, the individuals at the centre of the cluster, surrounded by other information parasites will quickly decline in fitness in a changing environment. However, as soon as one asocial learner appears, by mutation, inside the cluster, the fitness of its social learning neighbours jumps above the population average for asocial learners. This means that asocial learners are unable to re-invade once social learning is established, even though the global fitness of social learners is very low.

Edge effects around the clusters themselves are also of interest and drive effects like expansion and contraction of clusters. The social learners at the edge of the clusters interact with social learners inside and asocial learners outside. This means that they can, in effect, ferry new information into the centre of the social learning cluster. The leading edge of a social learning cluster therefore has extremely high fitness and so allows the spread of social learning despite low fitness at its centre

(Figure 2.2a). This low fitness persists, lowering the average fitness of the population as social learning extends its reach.

Clustering in evolutionary models in general seems to allow costly behaviour, usually open to exploitation by defectors, to persist in the population for a number of generations. This can be seen not only in social learning models but also in closely linked cooperation and niche-construction models (Nowak & May 1992; Hauert 2001; Silver and DiPaolo 2006). Chapter 2 highlights the possibility that social learning can propagate maladaptive information in a structured population especially in the centre of contiguous groups of social learners.

In the case of spatially structured models of niche construction (Silver and DiPaolo 2006) these spatial clusters were formed of a core of homozygote niche constructors (labelled as *AAEE*) with this homozygote core surrounded by a ring of individuals forced to interact and interbreed with the non-niche-constructing majority (*aaee* homozygotes). This process of mixing formed a layer of heterozygote individuals in the boundary regions of the clusters. The heterozygotes were able to support the immigration of *A* alleles into the boundary layer by manufacturing the resource which favoured this allele. This process allowed the accumulation of *A* alleles in the boundary layer, and through statistical association with these favoured *A* alleles, *E* alleles were able to increase in frequency where they would otherwise be driven to extinction. In this way the costly trait existed for a short time in poor conditions while the heterozygote layer improved the environment enough to subsequently favour its expansion. In other words, the niche-constructing traits hitchhiked to fixation through association with the recipient alleles that their activities favoured through selection. This model showed that the effects of spatial structure allowed niche-constructing alleles to evolve and spread in circumstances that the more traditional non-spatial models were unable to detect.

Chapter 7 continued this work with a spatial model of cultural niche construction, where a cultural bias for or against the niche-constructing trait was assessed with regard to the impact on the evolution of both niche construction and hitchhiking resource-dependent traits. This model focused on the same 'di-allelic' system with resource-dependent locus **A**, but the second niche-constructing locus **E** was conceptualized as a cultural rather than genetic trait, subject to cultural transmission biases. The model in Chapter 7 also added a further locus **B**, which represented a potentially costly genetic trait that could increase the underlying capacity for niche constructing. This can usefully be conceptualized as a capacity, such as a larger brain, that allows the individual to increase the rate or effectiveness of niche construction at some cost.

This cultural model yielded similar results to Silver and DiPaolo's model (2006), with the niche constructors initially forming clusters by chance, allowing the statistical associations to form between the recipient *A* allele and the niche-constructing cultural trait *E*. This happened because the assortative mating between neighbours meant that the increased resource frequency created by the *E* individuals favoured *A* alleles and thus favoured *E* through a positive feedback effect. The consequences of including spatial structure are also apparent here as the random global mating in the non-spatial model did not allow the build up of the statistical associations between *A* and *E* required for them to become sufficiently linked to drive this co-evolutionary cycle. The analysis also showed that the hitchhiking could still occur when levels of oblique transmission were low or moderate but that the effects broke down when oblique transmission was high, relative to rates of vertical transmission. The cultural-niche-constructing practice could also overcome some counter selection especially when a cultural bias in favour of the trait was in effect. In almost all cases considered, the effects of spatial structure were to increase the possibility of a niche-constructing trait spreading, and to allow the hitchhiking of recipient traits at other loci, over an extremely broad range of conditions, including costly alleles at the **B** locus that enhanced the niche-constructing capability. Thus niche-constructing traits could not only drive themselves to fixation but could increase their potency in the process.

The spatial model in this case reflects the kind of agriculture- or technology-driven ‘gene-culture co-evolution’ to which humans are thought to have been frequently subject (Laland 2010; Smith 2007; O’Brien and Laland *in press*). The heterozygote boundaries of niche-constructing clusters can easily be envisaged as an advancing wave of agriculture or technological adoption, such as that discussed by Kandler and Steele (2009) in their analytical reaction-diffusion models of similar processes. The important general point here is that spatial models have revealed potentially important processes that non-spatial models failed to detect.

Related models of the evolution of cooperation also show changes in evolutionary dynamics in spatial extensions of non-spatial models. Many models of cooperation are based on traditional games like the prisoners’ dilemma, snowdrift game or public-goods game. Here, we examine spatial extensions to models based on the prisoners’ dilemma and on the less well-known snowdrift game. The prisoners’ dilemma is traditionally a symmetric two-person game where the players have two possible moves: cooperate or defect. Ultimately the payoff structure of the game (Table 10.1a) means that it pays to defect regardless of what your partner does. The payoff matrix (Table 10.1a) shows that in a one-shot interaction, the only ESS is defection, not cooperation. However, when the game is altered to allow repeated interactions, and to allow agents in the game a perfect memory of their previous interactions, then strategies that can support the evolution of cooperation in certain circumstances emerge. In Axlerod's tournaments (Axelrod 1981), agents participated in just such an iterated prisoner's dilemma game. The tournament revealed that TIT-FOR-TAT, where agents retaliated when their opponent failed to cooperate but not before, was a good strategy - it won the second tournament despite the fact that entrants to the second knew about its success in the first. It was later shown that a TIT-FOR-TWO-TATS strategy (the sample strategy given to contestants by the organisers of the tournament to illustrate how to write a strategy), which would not defect until provoked by two defections from its opponent, could have beaten the original winner had it been entered (Axelrod 1984). One natural extension of this simulation framework was to introduce structured populations, making the traditional evolutionary games explicitly spatial.

Table 10.1: The payoff matrices for two evolutionary cooperation games

(a) Prisoners' dilemma	Cooperator	Defector
Cooperator	b-c (Reward)	-c (Sucker)
Defector	b (Temptation)	0 (Punishment)

(b) Snowdrift game	Cooperator	Defector
Cooperator	b-$\frac{c}{2}$ (Reward)	b-c (Sucker)
Defector	b (Temptation)	0 (Punishment)

Table 10.1: The payoff matrices for two evolutionary cooperation games where b is the benefit of the resource obtained through cooperating and *c* is the cost associated with cooperation. The matrix shows

the payoff awarded to an individual playing the strategy shown in the first column when playing against that shown in the first row. (a) Shows the payoff matrix for the prisoners dilemma where it pays to play the same strategy as your opponent, and (b) shows the payoff matrix for the snowdrift game where it pays more to play the opposite of your opponent's strategy in any given round.

One of the advantages of introducing this kind of spatial structure is that, as with other models, although the structure can be interpreted minimally as a geographic distance, it can also usefully be seen as a demographic structure of any sort that restricts free global interactions between individuals. This is an especially interesting distinction to make in this case since the kind of cooperation that we see outside of humans is often localised or directed towards group members or kin e.g. (Seyfarth 1984; Wilkinson 1984). In that way any conclusions that are drawn from the spatial models can be generalised and extended to include restricted interactions between other sub-groups within the population as a whole and can shed light on the effects of in- and out-groups on the evolution of cooperation.

Spatial effects in the evolution of costly behaviour like cooperation are generally thought to increase the likelihood of invasion and maintenance of strategies that would be more open to exploitation in well-mixed populations. While spatial models of the evolution of social learning seem to suggest that spatial structure may result in the spread of social learning despite the lowering of the average fitness in the population (Chapter 2), cooperation is not always supported by spatially structured populations, and is at times hampered by the presence of spatial structure, depending on the payoff structure of the game (Fu *et al.* 2010; Hauert & Doebeli 2004; Hauert *et al.* 2006). Nowak *et al.* (1994) show that spatial structure in stochastic simulations of iterated prisoners' dilemmas allowed cooperators to coexist with defectors without the need for complex strategies. This, in part, occurred because the cooperators were able to form spatial clusters, as with the social-learning and niche-construction models, this time avoiding exploitation by defectors. The impact of spatial structure on the maintenance of cooperation in a population is critically sensitive to the underlying update rule, as well as the payoff functions and structures. In the prisoners' dilemma, for example, the payoff structure (Table 10.1a) shows that it pays to mirror your opponent's move in any given interaction. This means that individuals in agent-based simulation models naturally congregate and segregate into groups acting in a similar way. The consequence of this grouping is that individuals form spatially explicit clusters dominated by particular strategies, helping the evolution of cooperation in these circumstances. The effects of spatial structure in these circumstances are especially strong.

In the spatial prisoners' dilemma, the chance of cooperators surviving in the population is independent of the actual number of original cooperators, but depends critically on their ability to form at least 3*x*3 clusters in space (Hauert 2001; Killingback *et al.* 1999; Langer *et al.* 2008). It remains to be seen to what extent these findings based on clustering are robust to more realistic assumptions about individual dispersal.

Although the clustering effect in Prisoners' dilemma models is pleasingly intuitive, the introduction of spatial structure leads to very different results in other strategic settings. This is illustrated nicely with the snowdrift game, another established window on cooperation. This game can be envisioned as two people trapped either side of a snowdrift. Each has two options, they can dig the snow or they can wait. If both dig, both get past the snowdrift, sharing the cost of digging. If both wait neither gets past. However if one person digs and the other waits, both get past the snowdrift but one shoulders the entire cost of digging the snow. This payoff matrix (Table 10.1b) leads to quite different dynamics to the prisoners' dilemma. In this case, it pays to do the opposite to your opponent in any given interaction. This force opposes the formation of clusters of either cooperators or defectors.

Hauert and Doebeli (2004) demonstrate a change in dynamics in the case of the snowdrift game as compared to the prisoner's dilemma. In the spatial snowdrift game the effect of spatial structure is to reduce the amount of cooperation sustained in the population compared to the non-spatial model and in some cases cause cooperation to go extinct. The clusters that form in the snowdrift game are diffuse, expanding 'dendritic structures' which expand as individuals vie to border those exhibiting a strategy opposite to their own. The 'pays to do the opposite' finding here bears some resemblance to the findings of Kylafis & Loreau (2008), who found that it only pays to niche construct to produce a resource when the manufactured resource is not otherwise available in the environment. The patterns that emerge from spatial models of cooperation, as has been shown in spatial models of ecology in the past (Rohani *et al.* 1997; Doebeli and Ruxton 1998), can be very interesting. They can be chaotic in certain cases with kaleidoscopic patterns emerging from non-stochastic runs of prisoners' dilemma simulations (Nowak & May 1992) or enter limit cycles of cooperation and defection (Hauert *et al.* 2008). Detailed examinations of other strategies that can compete within the hawk/dove or snowdrift type of model show that spatial effects can also support strategies that non-spatial models cannot and that incorporating social learning and cultural transmission of strategies can also support more cooperation in these systems (Killingback & Doebeli 1996).

Interesting comparisons can be drawn between the spatial models of social learning, niche construction and cooperation with regard to the shapes, sizes, functions and processes affecting the clustering of costly behaviour. The subtle differences in the mechanisms that bring and keep these clusters together can also help to elucidate the differences in the microscopic processes at work in each system. For example, groups of co-operators forming in spatial prisoners' dilemma games are held together by inward evolutionary forces, caused by the advantage to cooperating individuals of having cooperating neighbours. Conversely, social learning clusters are held together by the inability of asocial learners to survive where social learners surround them. Further examining the structure of these clusters could help us to identify the different processes causing successful or unsuccessful invasions of particular strategies into populations (Langer *et al.* 2008).

The spatial-niche-construction models restrict the benefits of niche-construction to the immediate locale of the constructor. It would be a natural - and fascinating - extension to consider allowing niche constructors to produce (or deplete) resources for (or produced by) their neighbours. Such an extension potentially takes such models into the sphere of spatial cooperation models and at the same time addresses the concern that models of cooperation have neglected ecological processes (Nowak *et al.* 2010). The inclusion of spatial and population structure in models examining the evolution of niche construction and cooperation, in particular, has also enabled more empirical and experimental testing of the models. Many tests have now been performed using bacteria in media allowing or restricting free mixing of individuals and sharing of resources. This paradigm has been used to examine the evolution of cooperation e.g. (Kummerli *et al.* 2002; LeGac & Doebeli 2010) and niche construction (e.g. Kerr *et al.* 2002) and would have been difficult or impossible to interpret correctly in the light of purely non-spatial models.

The primary advantage of extending models to include the effects of spatial (or demographic) stratification is realism, and therefore, validity (although a critic could justly complain that the cellular automaton approach is a very crude approximation of natural spatial structure (Holland *et al.* 2007) or that the patterns generated by non-stochastic models are not robust to perturbation (Hanski 1994 but see Rohani *et al.* 1996)). Nonetheless, it is abundantly obvious that we live in a spatial world. We interact differentially with individuals who live and work in our neighbourhoods, we interact less with those who do not. This is, of course, by no means a strict rule and further generalisations of the models discussed above could usefully look at a more 'small world' type of stratification (Watts 1999) where the likelihood of interacting with distant members of the population is greater than zero or that incorporate levels of dispersal that better capture biological reality. There is now considerable evidence that many societies operate in a 'small world' way (Watts 1999) and evidence from ethnographic studies of information flow in a number of settings suggest that people teaching or demonstrating skills to others restrict their demonstrations either knowingly or inadvertently to kin. For example, the adze stone tool knappers in Indonesian Irian Jaya restrict access to their highly structured stone tool apprenticeships to their sons or nephews (Stout 2002), Kpelle children in Liberia, while not consciously taught, learn preferentially from their own parents due to near-constant spatial proximity (Lancy 1996), and Aka Pygmies in the Congo restrict their learning role models to parents, grandparents or highly skilled others (Hewlett and Cavalli-Sforza 1986). Both the formal and informal restrictions on learning role models in these cases mimic, to an extent, the spatial structure the models impose.

The models discussed here are simulation models but this does not have to be the case: some spatial systems can be modelled using equations like reaction-diffusion equations or spatially implicit analytical models (e.g. Levins & Culver 1971). These models have the advantage of eliminating the problem that spatially explicit agent-based models necessarily disallow continuous time processes. Discrete time and updating rules in these models have been shown to change results of evolutionary simulations considerably (Huberman & Glance 1993). The advantage of using the simulation approach, though, is that it is relatively easy to extend non-spatial, analytical descriptions of different systems to account for the effects of spatial structure without redesigning an entire model from scratch and without reducing the ability to compare between spatial and non-spatial results.

The fact that the results from spatial models differ, sometimes substantially, from their non-spatial ancestors, coupled with the fact that spatial stratification is observable in most animal systems means that these models may more accurately reflect the environment in which animals, ourselves included, learn and evolve. This, in turn, may mean that the most informative models are by necessity spatially explicit ones.

The Implications of Mechanism and Strategy for Culture

Chapter 3 presents a model of the evolution of teaching. The definition of teaching used here is a variant of the functional definition of teaching proposed by Caro and Hauser in 1992 where a tutor is said to teach if it modifies its behaviour in the presence of a pupil, at some cost, thereby promoting the pupil's learning. Proposed refinements of this definition have imposed additional criteria, such as feedback from pupil to tutor, or restrict teaching to the transfer of skills, concepts and rules (Franks and Richerson 2006; Leadbeater *et al.* 2006; Hoppitt *et al.* 2008). The definition implies that teaching can usefully be described as a costly behaviour that functions to increase the fidelity of information transmission. Although this functional definition of teaching is widely used and accepted in the animal behaviour literature (Thornton and McAuliffe 2006; Franks and Richardson 2006; Leadbeater *et al.* 2006), more recently it has attracted some controversy for ignoring the cognitive processes underlying teaching and focussing too narrowly on the functional aspects (Byrne 2011). The controversy arises largely from a difference in research focus. The functional definition, in Byrne's view, hinders research into the origins of the complex cognition required for human teaching, and a more cognitive definition of teaching including the need for mental state attribution, clear intention on the part of the teacher and deep understanding of their actions, would make research into non-human animal teaching impossible (Caro and Hauser 1992).

The advantages of using the functional definition of teaching in the model presented in Chapter 3 are multi-fold. First, the definition proposed by Caro and Hauser (1992) sets out three simple and observable criteria (a change in behaviour in the presence of a pupil, a cost to this change and increased efficiency of learning on the part of the pupil), which lend themselves easily to both measurement and mathematical treatment. Second, using this definition allows the model to describe non-human teaching and with extensions, to elucidate the evolution of more complex human teaching. Third, and importantly, as the evolutionary origins of human teaching are unknown, cognitive definitions are in danger of making unsupported assumptions about the evolution of other human cognitive traits and the ability to teach. This is especially important when modelling with the aim of uncovering these evolutionary origins and identifying aspects of human cognition, like the capacity for cumulative culture that may have coevolved with teaching.

High-fidelity information transmission has been shown to be critical in maintaining important features of human culture like cumulative cultural evolution (Enquist *et al.* 2010; Ehn and Laland 2012; Lewis and Laland *in press*), and in maintaining animal traditions (Whiten *et al.* 2007) (although other transmission mechanisms like emulation are often invoked in discussions of animal traditions)

(Hopper *et al*. 2008; Tomasello 1999). Chapter 3 shows that in models of teaching that allow for cumulative cultural knowledge gain, the fitness benefits of teaching increase with the ability for cumulative culture, and that individuals engaging in cumulative culture in a population where teaching is very effective reap higher fitness benefits than those in low teaching efficacy populations, again showing an important link between teaching and cumulative culture and hinting at a possible co-evolution between cumulative culture and teaching. This link between teaching (and other high-fidelity mechanisms) and cumulative culture has recently been demonstrated experimentally (Dean *et al.* 2012). By virtue of our capacity for language, pedagogical cueing, teaching through imitation, manual shaping, and mental state attribution, which allows tutors to adjust their teaching to the state of knowledge of the pupil (Premack 2007; Tomasello and Call 1997), the fidelity of human teaching is likely to be high relative to the fidelity of teaching in other animals who teach through simple means, such as opportunity providing (Tomasello 1994; Csibra 2007; Csibra and Gergely 2006).

Although it is likely that the full taxonomic distribution of cases of animal teaching is incomplete (Hoppitt *et al.* 2008; Thornton and Raihani 2008; Laland and Hoppitt 2003), it is undeniable that the generality and pervasiveness of human teaching is in striking contrast to teaching in other animals. While some researchers have claimed that teaching is not in fact ubiquitous in human societies (Whiten *et al.* 2003; Whiten and Milner 1984) it is clear that this distinction refers to directly spoken formal instruction and does not take account of non-verbal instruction and more subtle forms of teaching like pedagogical cueing (Hewlett *et al.* 2011). For example, Hewlett and Cavalli-Sforza (1986) show that while the Aka Pygmies are not formally educated, they learn by observation combined with 'instruction' through 'the few things the educator did or said to transmit the skill or knowledge'. Although teaching in post-industrial societies is ritualised, formal and in the vast majority of cases, verbal, this may not be the case for teaching in most human societies. Nonetheless, teaching in some form seems to be present.

In contrast to human teaching which covers a staggering array of topics and skills, animal teaching is typically narrow in scope often concentrating on one trait or trait type (for example, food processing in meerkats). Nonetheless we do see teaching behaviour, however narrowly applied, in a number of animals. The taxonomic distribution of these putative cases of teaching seemingly does not follow the taxonomic distribution of animal intelligence as measured in lab-based experiments.

The findings outlined in Chapter 3 shed light on the taxonomic distribution of teaching in three important ways. First, they explain the narrow scope of animal teaching and suggest that the specific behaviours that are taught by animal teachers are the few that satisfy the stringent criteria suggested by the model. If the behavioural traits are too difficult to pick up either through inadvertent social learning or through asocial learning, at invasion, teachers are unlikely to have the information available to pass on to their pupils and the advantage to teaching disappears. If the behavioural traits are too easy to pick up through means other than teaching, there is little point in investing time and energy in teaching, as other cheaper forms of learning would be just as effective. This explains why there is no straightforward relationship between brain size measures or cognitive capabilities and the ability to teach: animals good at inadvertent social learning and innovation will pick up information through means other than teaching. Moreover, there typically needs to be a substantive fitness advantage to acquiring the taught information for teaching to be favoured. For example, in the case of meerkats, there are high risks of injury from dangerous prey items like scorpions, which constitute about 4.5% of the adult meerkat diet, if individuals do not learn how to safely process them (Thornton and McAuliffe 2006). The fitness benefit of learning to process these items is therefore likely to be large.

Second, the model found that high relatedness in a population is key to the evolution of teaching, with the likelihood of teaching evolving increasing with the degree of relatedness between pupil and teacher. The increase in relatedness between pupil and teacher also increases the likelihood that an individual with a teaching genotype will be taught and increases the inclusive fitness benefits of teaching. This could help to explain the presence of teaching in social insect species like tandem running ants and social bees (Franks and Richardson 2006; Leadbeater *et al.* 2006; Hoppitt *et al.* 2008; Thornton and McAuliffe 2006) who are generally thought to have higher relatedness among foraging individuals (Cornwallis *et al.* 2010).

Third and finally, the model suggests that a low *per capita* time investment in teaching would also facilitate the evolution of teaching. Cooperative breeding (which is often linked to high relatedness, see Cornwallis *et al.* 2010) can cut the *per capita* time cost of teaching and increases the inclusive fitness benefits. Relative to non-cooperative breeders, cooperative-breeding helpers engage in more costly and prolonged provisioning of young (Thornton and McAuliffe 2006; Langen 2000). It is possible that in cooperative breeders, the sharing of costs amongst multiple tutors corresponds to a significantly lower time cost to an individual teacher, which in turn makes teaching more economical and more likely to evolve. Teaching may be favoured only where the tutor's operational costs are low, and indeed there is evidence that investment in teaching is proportional to health-related state variables in meerkats (Thornton and Raihani 2008). It may be no coincidence that teaching is disproportionally observed in cooperative breeding species (Thornton and Raihani 2008).

Fidelity of information transmission was also an important factor in the models presented in Section 2, which examined the implications of the Social Learning Strategies Tournament for cultural evolution. The tournament (Chapter 4) drew attention to the possibility that, in addition to asocial learning, copy error represents another possible avenue through which new information could enter a population. This is in ways analogous to mutation in genetic evolution: the vast majority of mistakes are deleterious but some confer fitness benefits (Muller 1950; Lande 1994). This raises a possibility: to the extent that copy error represents a useful source of new information, this may act as a selective pressure *against* high fidelity transmission. However it is clear that in the melee, which is arguably the most biologically plausible simulation condition in the tournament, new information was provided largely by the asocial learning that some strategies exhibited. This meant that copy error was not needed in order to track the environment. In the cases where copy error did occur, it was less likely to generate high-payoff information than accurate copying since the payoffs for behaviours were exponentially distributed and demonstrated behaviours were typically selected by effective strategies for their high payoffs. Thus, except in circumstances where there is no other source of new information present, or the rate of environmental change is high, it is likely that selection will favour high-fidelity transmission.

More generally, the tournament generated a number of surprising results. First, the tournament showed that copying was adaptive under a broader range of conditions than was predicted by other theoretical work (Boyd and Richerson 1985; Rogers 1988; Feldman *et al.* 1996; Enquist *et al.* 2007). By choosing high payoff behaviour, individuals inadvertently filtered the information available in the population, so that in the pool of behaviours made available to copy through exploitation, high-fitness variants were over-represented. Second, the tournament showed that in the presence of some source of new behavioural variants, social learning did not lead to the fitness depression seen in Rogers' paradox models. This was, in part, the result of the availability of a wider repertoire of behaviours. The repertoire meant that individuals could switch to new, higher fitness behaviours in times of environmental change. This led to the result that copying could pay, even in a highly changeable environment.

There is some evidence that the strategies that were successful in the tournament are found in more natural settings, for example in social insect learning (Grüter *et al.* 2010). Foraging social insects face a scenario much like the one posed in the tournament simulation environment. Foraging insects must choose whether to learn the location of a new food patch by watching others (in the case of honey bees through watching waggle dances), learn by searching for foraging patches individually or use their memories of previous flights to visit a foraging patch the location of which they were already familiar with. These actions correspond to learning through OBSERVE, learning through INNOVATE or playing EXPLOIT respectively. Grüter *et al.* (2010) found that both honey bees (*Apis mellifera*) and wood ants (*Formica rufa*) learn (either through independent foraging or observation of conspecifics) and exploit the resources they find until they become unprofitable, at which time they cease exploiting and resume learning. For example, honeybee foragers attend to waggle dances significantly more when a previous patch has recently declined in quality as a result of environmental change than at other times (Seeley and Town 1992; Biesmeijer and Seeley 2005). In the tournament this kind of action would correspond to timing learning moves to environmental changes and a drop in payoffs, something that was critical to overall success in the tournament.

The tournament analysis presented in Chapter 5 sheds some light on the evolution of certain features unique to human culture. The analysis showed that many features of human culture such as high diversity of cultural traits, high trait longevity and rapid turnover in behaviour (evocative of fads and fashions) can emerge from a simple model of social learning as reliance on social learning increases, provided there is some source of new information. In fact, the tournament has proven an effective means of exploring a number of questions and paradoxes concerning cultural evolution. By illustrating the striking utility of copying across such a broad range of conditions, and drawing attention to the adaptive filtering performed by individual agents, it helped to explain why social learning is widespread in nature. By isolating the factors that lead strategies to be successful, the tournament has made a series of predictions as to the patterns of strategic copying likely to be observed in nature (e.g. copying should increase when payoffs drop, but rapidly drop off once effective behaviour is found).

A focus on the winning strategy leads to the insight that mental time travel, combined with the ability to estimate rates of environmental change, may be a vital feature of human copying, since it not only allows individuals to discount old information but also allows individuals to assess the likely utility of current information in the future (see Chapters 5 and 6). The winning strategy computed whether further learning would likely lead to new behaviour with high payoff being brought into its repertoire. These analyses also help to explain how a highly culturally dependent species like humans might accumulate large amounts of cultural knowledge, when copying is generally thought to lead to behavioural homogeneity.

The key here is a distinction between cultural knowledge and behaviour. Provided copying errors or innovation introduce new behavioural variants, copying can simultaneously increase the knowledge base of a population, and reduce the range of exploited behaviour to a core of high-performance variants, which efficiently track changing environments. Similar reasoning accounts for the observation that copying can lead to knowledge being retained over long periods of time yet trigger rapid turnover in behaviour. Low-level performance of sub-optimal behaviour is sufficient to retain large amounts of cultural knowledge in copying populations, over long periods. Indeed, a high level of copying was associated with an increase in the retention of cultural knowledge by several orders of magnitude.

The tournament also showed that the timing of learning moves (shown to be in part mediated by efficient and intelligent use of memory in Chapter 6) was critical. Those strategies that scored badly in the tournament used social learning randomly with respect to time, failing to match their learning moves to the changes in environmental conditions. In this case there was a negative correlation between use of social learning and tournament score. In short, social learning only paid when it was used at strategically chosen times. Since both strategic timing and memory-use have been shown to increase fitness benefits accrued to social learners they can join the ranks of solutions to the paradox of non-adaptive culture. The implications of this finding are potentially wide reaching. It may be the case that social learning has increased the fitness of the human species, contributing to our huge ecological and demographic success, precisely because we have a highly enhanced capability to use social learning strategically not only with respect to *who* we choose to copy, but critically with respect to *when* we choose to copy. It is likely that without the cognitive capacity for high-fidelity transmission, teaching, imitation, language and mental time travel, our species may never have reaped the full benefits of cultural transmission and social learning.

Modelling the Complexities of Human Culture

Chapters 7 and 8 are general models of niche construction, one in a finite population of stochastic, spatially distributed agents and another in an infinite-sized population with deterministic dynamics. Generating general models enables researchers to investigate a number of phenomena using a common framework, makes comparison between systems possible, enabling researchers to compare the effects of similar parameters on different systems meaningfully, while more precise models allow accurate quantitative results and hypothesis testing.

In the case of population biology, Levins (1966) claimed that there were three approaches to modelling: to sacrifice generality to realism and precision, to sacrifice realism to generality and precision and finally to sacrifice precision to realism and generality. The models presented in this thesis make simplifying assumptions about how animals learn and transmit genetic predispositions to engage in learning or niche construction, at the cost of realism. For example, the assumption in Chapter 3 that teaching is a monogenetic trait is incorrect, but the model assumes that it is a good approximation of the truth and that small deviations from realism cause only small deviations in conclusions. The first approach of sacrificing generality to realism and precision was used in Chapter 9 and is the approach that most lends itself to models informing policy. The shortcomings of this approach are the same for models of cultural evolution as they were for population biology, both in terms of generating values for the numerous parameters such detailed modelling requires, and in generating solvable equations. As Levins points out, such complex models are rarely, if ever, analytically soluble. However, the problem of solubility becomes less important as more powerful computers become available to make numerical estimates of solutions, and happily it is the case that models that were completely intractable when Levins wrote his 1966 paper are now tractable on little more than a desktop computer.

It is not always necessary, however, to have precise models and in the chapters where it is more interesting to look at qualitative rather than quantitative results, precision must necessarily be sacrificed. The model in Chapter 8 is a general model of cultural niche construction with applications to a number of systems. The discussion in Chapter 8 draws attention to three such applications: the coevolution of religion and fertility, the cultural evolution of son preference in China and the cultural evolution of human large-scale conflict. Using this model it is possible to identify (within the bounds of the model's assumptions) the long-term dynamics and evolutionary outcomes of the systems.

One of the most interesting outcomes of this model is the way in which its findings contrast with the findings of Rowthorn (2011). Rowthorn modelled the evolution of fertility and religion, claiming that the endogamy typical of religious groups combined with higher fertility meant that (if there is, in fact, such a thing) any genetic predisposition to religion must inevitably fix in the population. In the discussion of his findings, Rowthorn (2011) notes that this may lead to a society in which most individuals are religious and where those individuals who, despite having a predisposition toward religion, are not religious, are likely nonetheless to have the associated traits of social and political conservatism. Rowthorn's model suggested that human society is on an irreversible path towards the only possible outcome: complete religiosity coupled with complete conservatism.

The model presented in Chapter 8 relaxed some of the more stringent assumptions of Rowthorn's model, the most important of which was complete assortative mating. It was found that even a slight relaxation of the assumption of complete endogamy in religious groups led to very different results. Analysing the model involved examining a wide parameter space and running millions of simulated parameter sets. The analysis found that a number of alternative equilibria existed. These included coexistence of religious alleles and non-religious alleles as well as the extinction of religiosity, the opposite of Rowthorn's finding. It would seem that Rowthorn's strong assumptions, coupled with a model that did not sufficiently explain the feedback between interacting traits, generated a prediction that was in fact just one of a number of possible evolutionary outcomes.

One recent study of religious endogamy and interfaith marriages (Heaton 1990) showed that the rate of men marrying outside their religion was greater than zero (note, since the model presented in Chapter 8 arbitrarily assigned males as the 'choosing' parent, the rate of men marrying outside their religion in each particular religious group is taken into account here). The rate of interfaith marriages among the religions surveyed ranged from 8.6% among members of the Reformed Church (translating into an endogamy rate of 91.4%) to 38.2% among Presbyterians (translating to an endogamy rate of 61.8%). The value range $0.618 \leq \alpha_1, \alpha_2 \leq 0.914$ for the assortative mating parameters (α_1, α_2) fits closely with the range for which the model predicts polymorphisms ($0.6 < \alpha_1, \alpha_2 < 1$).

The success of the cultural evolution literature in explaining important aspects of human society and behaviour has the potential to lead the field in new directions. Cultural evolution is now becoming an extremely useful tool for explaining the complex forms that our cultures take (e.g. Bowles 2000; Lipatov *et al.* 2011; Shennan

2011; Lansing and Fox 2011). An interesting test case for cultural evolution is the persistence of son preference in much of Asia and North Africa despite a dangerously high sex ratio at birth (SRB). In Chapter 9, I present a model of the cultural evolution of sex-ratio bias and marriage practices in China. The model was created with a view to providing insights into how best to return the sex-ratio in China to, or close to, natural levels. The model aimed to describe possible policy interventions such as initiating pro-daughter advertising campaigns, increasing access to education in low socio-economic sectors or relaxing the stringent controls on reproduction in urban China, and quantify their relative effects on the SRB according to the assumptions of the model. The utility of this model and others like it (e.g. Li *et al.* 2000; Lipatov *et al.* 2011) rests critically on the anthropological data that informs them. Three fundamental aspects of the model presented in Chapter 9 are the estimates made by anthropologists and economists of (1) the SRB as it currently is in affected areas, (2) the expected SRB in the absence of discrimination, and (3) the number of ‘missing women’ resulting from differential food and medical care in early life, infanticide and sex-selective abortion.

Estimating the number of missing women, though not directly relevant to the model presented in Chapter 9, is nonetheless extremely important as it is this figure along with investigations into the societal problems associated with excess males (e.g. Ebenstein and Sharygin 2009; Li *et al.* 2000; Tuljapakur *et al.* 1995) that encourage researchers and policy makers to investigate and target the problem. The estimates of SRB come primarily from census data, sometimes from inter-census surveys where they are available, and from other, smaller-scale surveys conducted by research groups and demographers. Census data remains the most complete and accurate source of data on the SRB but both Chinese and external demographers have played a crucial role in tracking the spectacular rise of the SRB in China since the 1960s (Croll 2000). Accurate estimates of the SRB past and present enable more accurate estimates of the effect of policy interventions on the future SRB.

One of the most contentious issues involved in estimating the number of missing women is first estimating the expected SRB (s_0) in the absence of gender discrimination against girls. In 1990 Amartya Sen used the prevailing sex ratio in sub-Saharan Africa as an approximation of the expected sex ratio throughout Asia and North Africa where the skew in SRB is most pronounced. This was a sensible starting point and was designed to give the readers an idea of the severity of the discrimination he was describing. Sen estimated that there were 107 million missing women worldwide, an estimate that has been revised upwards to 108.9 million since 1990, using more up to date estimates of his parameters. Coale (1991) suggested that the demographic differences between sub-Saharan Africa and Asia were too large to use one to estimate the other legitimately. Factors like the death rate, birth rate and naturally lower sex ratios in sub-Saharan Africa meant that the s_0 value in Asia was likely higher than that estimated by Sen (1990). In order to account for these demographic factors, Coale suggested using ‘Regional Model Life Tables’ to estimate the likely value of s_0 in the affected countries. In all four Model Life Tables (East, West, North and South) there is a higher male mortality rate relative to female mortality, which erodes the naturally higher number of males at birth leading to a roughly 1:1 sex ratio in later life (although the exact timing of this convergence is a function of mortality and age structure).

The model analysis presented in Chapter 9 uses a value of s_0=1.05. This value is a defensible one, since Klasen and Wink (2003) showed that most countries without this kind of gender discrimination have values that lie between 1.03 and 1.06 and that

China specifically has a value of exactly 1.05, based on the use of the 'East' model life tables. The model itself remains open to the use of other values, which would change at least the quantitative outcomes of the model. The estimated number of 'missing women' is then generated by using the value of s_0, and natural female mortality rates to calculate the missing proportion of women which is 6.7% in China (Klasen and Wink 2003).

The model describes the interaction between marriage practices and son preferences in a number of socioeconomic sectors in modern China. While the analysis considers policy implications, the model also adds something to the general cultural evolutionary literature. While Carotenuto *et al.* (1989) and Li *et al.* (2000) introduced cultural evolution to standard demographic Leslie matrix models, the model in Chapter 9 used similar methods to add both age and socio-economic structure to the cultural evolution model. This meant that the model could investigate how a change in the cultural beliefs of one socioeconomic sector could change the sex ratio in others. It was also able to investigate the effect of increasing access to education for girls in the lowest socioeconomic sectors for women in the highest. The fact that socioeconomic status is highly correlated with urban/rural location in China coupled with the fact that urban/rural location is strongly correlated with the strength of enforcement of the one child policy, means that ignoring socioeconomic status, and the different rules to which rural and urban families are subject, would belie the true complexity of the situation in China. The model in Chapter 9 implies that targeting advertisement campaigns at high socioeconomic status, urban families is less likely to change the national sex ratio than improving access to education for girls in low income rural areas. This distinction would be impossible to make without specifically modelling the effect of age, socioeconomic status and cultural transmission. It is possible that there are many other human cultural systems that would benefit from this combination of analyses, and still more that would benefit from other combinations of traditional models and cultural evolutionary analysis.

A potential application of this kind of combination is in traditional SIR epidemiological models of sexually transmitted diseases like HIV, which consider risk categories of individuals – those who frequently engage in risky behaviour and those who do not. Individuals within these risk categories contract the disease at different rates. Recruitment to risk categories and turnover in population sizes in those categories are treated as constant probabilities (Garnett 2002; UNAIDS 2009). However, movement of individuals between groups engaging in risky behaviours is more likely to be mediated, as with other cultural practices, by a combination of vertical, horizontal and oblique influences on cultural transmission. A similar modelling approach could be used to model the cultural transmission of anti-retroviral use or use of condoms in treating or controlling the spread of the disease. There are a large number of potential cultural influences on the transmission of HIV (Hrdy 1989) and other sexually transmitted diseases and it is possible that modelling them using appropriate cultural transmission models could significantly improve our estimates of the epidemiology of these diseases and predictions about their spread. The reality is that the cultural environment an individual lives in ultimately influences almost every aspect of their behaviour and we will not understand human behaviour without at least a cursory understanding of the cultural pressures shaping it.

More generally, the models presented in Chapters 8 and 9 show that while general models are useful in understanding the dynamics of cultural evolution and possible evolutionary endpoints, investigating specific problems associated with policy implementation typically requires a finer focus on the exact interactions between age, socioeconomic status, access to education and other important traditional customs.

The human species and its ancestors have undergone a huge transformation over the last six million years. We have moved from a life history very like Chimpanzees, Gorillas or Orang-utans, to one that is hugely rich and complex, so far removed from our ancestors that some members of our species actually doubt our evolutionary connection to the other great apes. The work presented in this thesis supports the view that this transformation began with social learning and cultural evolution (Boyd and Richerson 1985; Richerson and Boyd 2005). Our ability to refine and improve the way we learn from each other through teaching, imitation and mental time travel, along with the ability to shape our cultural and ecological surroundings as they shape us, is the very foundation of what makes us unique as a species. As we face large-scale conflicts between cultural groups, and devastating destruction of our planet through culturally mediated over-consumption, it is possible that understanding and shaping our cultural landscapes is the biggest challenge that now lies before our species.

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