Advances in the Evolutionary Analysis of Human Behaviour

Mhairi A. Gibson
David W. Lawson *Editors*

Applied Evolutionary Anthropology

Darwinian Approaches to Contemporary World Issues

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Foreword

Monique Borgerhoff Mulder

There is a new confidence in the social and biological sciences in the value of our work, and nowhere is this more apparent than in the emergence of "evidence-based" fields. In the wake of the successes of evidence-based medicine (Sackett et al. 1996), in conservation biology we now have evidence-based conservation (Sutherland et al. 2004), in economics something fast approaching evidence-based development economics (Banerjee and Duflo 2012), and in policy the stirrings of similar movement (Biglan and Cody 2013). Sharing a commitment to systematic comparison, whether this be based on randomized controlled interventions (Cohen and Dupas 2010) or, where experimental manipulation is impossible, tightly controlled comparison (Andam et al. 2008), systematic reviews and meta-analyses (e.g. Brooks et al. 2012), these fields provide rigorously-assessed, and often widely vetted, knowledge for deployment in direct action.

So where are we with respect to an evidence-based evolutionary anthropology? The dozen chapters in this stimulating collection offer some intriguing pointers towards where we should be going. Clearly "behavioural change", the holy grail of so many conservation and public health projects, cannot be attained, either through educational interventions or restructured incentives, without a genuine understanding of how and why humans behave as they do. How can you change a person's firewood collection practices or health-seeking strategy if you do not understand the dynamics entailed in how ecology and individual circumstance shape opportunities and constraints, how opportunities and constraints shape preferences, and how preferences influence decisions? Furthermore, it is equally critical to understand the principle avenues whereby behaviour and ideas are transmitted between individuals if campaigns, pamphlets and educational outreach are to have any effects.

As many of the contributors to this volume make abundantly clear, behavioural ecology (the dominant framework of evolutionary anthropologists), and the evolutionary social sciences more generally, offer a powerful framework for tackling these issues, given their commitment to both distinguishing explanations of ultimate function from those of proximate mechanism and determining universal rules

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that underlie the diverse patterns of behaviour within and between different human populations. By examining decision-making within the matrix of the costs and benefits that structure the marginal returns to fitness associated with any particular action (or inaction), behavioural ecologists can develop hypotheses for how and why humans behave as they do, given a particular set of environmental opportunities and constraints. As a rigorously empirical discipline, these predictions are then tested with data from multiple populations in different parts of the world, with the objective of revising model assumptions (Borgerhoff Mulder and Schacht 2012). Furthermore, by using evolutionary models to identify, explore and describe theoretically-informed proximate triggers of behaviour, evolutionary social scientists should be in a position to design effective policy interventions. And then, with additional input from cultural evolutionary theory (Mesoudi 2011), they can identify key influences on how certain patterns of behaviour are transmitted within and between generations.

From the chapters in this volume we now know, for example, of extrinsic mortality's role in shaping reproductive and health decisions, of the salience of habit forming, of the highly contingent patterning of cooperation and punishment across human populations, and of the dangers of using simple models based on the assumption that individuals strive to maximize resource acquisition when we design strategies for reducing poverty. Are we ready to make evidence-based recommendations? Certainly some of the contributors to this volume are willing to move in that direction, always with caution given both past and present misuses and/or misinterpretations of evolutionary reasoning. Where we are typically lacking, however, is in clear policy recommendations. It is one thing to say 'We now know X, and this should guide policy' and quite another to say 'Knowing X leads us to recommend policy Y'.

To do this we need more evolutionary political science—a field largely missing from this collection because it is still so young. For example, it is certainly useful to know that the poor invest little in health care (their own and that of their children) not simply because of their limited finances but because of their high vulnerability to extrinsic sources of mortality and their consequential heavy discounting of future states of health. But this is only a start, and we need more ideas: to get policies which motivate people living in deprived neighbourhoods to find innovative ways of reducing extrinsic risk, which provide tax monies for the material and social capital to do this, or which offer incentives for those who wish to find new homes in less risky environments. These are fundamental policy shifts that change the structural parameters of inequality. They require ideological shifts in tolerating inequality that seem to occur more naturally in some contexts than others (Borgerhoff Mulder et al. 2009), but we still do not understand exactly why. Scientists are rarely good politicians. But by blending the insights of models, experiments, and systematic empirical comparisons, in the way Ostrom (2007) pioneered in the field of natural resource management, we need to start thinking about establishing a more comprehensive evidence-based social science.

So, to avoid being hoisted on my own petard, how do we as evolutionary anthropologists do this? The suggestions are deceptively simple. First, we should strive for greater communication with on-the-ground organizations dedicated to improving public health, alleviating poverty and finding sustainable use of natural resources; this is critical because these organizations typically have much greater access to policy-makers than do academics. We should also aim to integrate academic research more closely with project evaluation, as is occurring so successfully in development economics (e.g. Palm et al. 2005). It is also very important to make the results of our research accessible to those in the executive branches of government who can make best use of them. That said, being effective in any of these goals is difficult, and we still have many lessons to learn. Hopefully these chapters will attract new interest and fresh talent.

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Chapter 1
Applying Evolutionary Anthropology to a Changing World

Mhairi A. Gibson and David W. Lawson

Abstract Evolutionary anthropology presents a powerful theoretical framework to understand how both current environments and legacies of past selection shape human behavioural and cultural diversity. Combining ethnographic, economic and demographic methods, this integrative and pluralistic field has provided new insights into the ultimate motivations and proximate pathways that guide human adaptation and variation. In recent years, anthropologists and related social scientists have also begun to explore how evolutionary theory may be used as a tool to address questions of public health and social policy relevance. This marks a watershed development in evolutionary approaches to human behaviour, as the field moves beyond purely academic boundaries and into the realm of applied social science. As a species, we are currently experiencing dramatic shifts in our lifestyle, family structure, diet and health and global contact. 'Applied evolutionary anthropology' (AEA) can provide new insights into the causes and the consequences of such human behavioural shifts by studying populations at the cusp of these transitions. It also holds great, largely untapped, potential to guide the design, implementation and evaluation of effective social and public health policy. This edited volume reviews the current state of the emerging field of AEA, highlighting the work of a number of interdisciplinary evolutionary scientists studying contemporary world issues. In this chapter, we briefly introduce the objectives and main contributions of AEA, and discuss the key research themes explored both in this book and the wider literature.

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1.1 Introduction

> An anthropologist's primary duty is '*to present facts, develop concepts [and] destroy fictions and empty phrases, and so reveal relevant active forces*' (Bronisław Malinowski, cited in Firth, 1981, p. 195).

Anthropologists have a long history of acting as two-way communicators between local peoples and external global agencies/forces. The early goals of anthropology were not only to provide an explanation of the behaviour of unfamiliar and 'exotic' peoples, but also to present the 'native' view, highlighting local concerns to administrators and policymakers to facilitate better governance (Sillitoe 2007). With the wane of colonialism and the emergence of global communication networks and development aid, the significance of this dual role has grown (Crewe and Axelby 2013; Mosse 2013). Many anthropologists today seek to both identify and communicate the needs of peoples to policymakers (with the aim of ensuring culturally appropriate and effective forms of development), but also to address a range of issues affecting communities across a rapidly changing and increasingly globalised and interconnected world.

Since the early twentieth century, some anthropologists and social scientists have employed evolutionary theory to provide new insight into the behaviours of contemporary peoples, in both 'traditional' and 'Westernised' societies. Developing from the natural sciences, evolutionary anthropology argues that human biological and behavioural diversity and change result from variation, inheritance and adaptation to specific environments. This approach has improved our understanding of how local ecologies (both physical and cultural environments), legacies of past selection and current reproductive goals can explain human diversity (for recent reviews, see: Nettle et al. 2013; Brown et al. 2011). Informed by these Darwinian principles, and ongoing theoretical developments in evolutionary biology, a new generation of evolutionary anthropologists have begun to address a range of questions relating to human health, social welfare and public policy.

The aim of this edited volume is to highlight the work of those researchers who are currently using the theoretical framework of evolutionary anthropology to both deepen our understanding of human behaviour and help the people with whom they work. They seek to apply evolutionary principles to a range of issues of relevance to public health and social welfare. This includes not only identifying the concerns and needs of marginalised or disadvantaged peoples, assisting with the design and critique of policies which seek to implement changes to environments or in behaviour(s), but also addressing problems facing industry, government and society more widely. In many instances, this work not only addresses long-standing and unsolved human issues (e.g. how to solve cooperative dilemmas, mitigate risk and encourage positive health behaviours), but also stimulates research on new topics relating to dramatic recent changes in lifestyles and ecologies.

1.1.1 Why now?

We believe an appraisal of 'applied evolutionary anthropology' (AEA) is timely for a number of reasons. Firstly, the number of academic researchers explicitly addressing evolutionary explanations of human behaviour, within and outside of anthropology, has grown substantially in recent years (Nettle et al. 2013; Brown et al. 2011), perhaps particularly with regard to evolutionary models of cultural transmission (Mesoudi 2011). Researchers are increasingly seeking to demonstrate the value of an evolutionary approach to neighbouring disciplines, extending beyond the core academic objectives to address applied concerns regarding human well-being (e.g. Tucker and Rende Taylor 2007; see also Diamond 2012, Sloan Wilson 2011, for recent more popular accounts). Similar commitments to applied research can also be seen in the overlapping fields of biosocial anthropology (Panter-Brick and Fuentes 2009), anthropological demography (Kertzer and Fricke 1997), evolutionary medicine (Nesse and Stearns 2008; Stearns et al. 2010) and evolutionary psychology (Roberts 2011). Such enthusiasm is paralleled by an increasing acceptance across the human sciences that evolutionary considerations can complement and substantially deepen our understanding of (both the ultimate and proximate) factors underpinning human decision-making and behavioural diversity. Furthermore, the value of anthropological expertise and cross-cultural comparative research have also become more readily acknowledged within psychology and economics (e.g. Henrich et al. 2010), disciplines that often have more (in)direct influence on social policy. All of these developments indicate that the emerging and integrated field of AEA is in good health and the intellectual climate is receptive.

A second factor is that there are clear signs that governments, charitable organisations and those social scientists working on the front line of global health and economic development policy are in a reflexive mood. Numerous, and often controversial, popular books, highlighting the mixed success of international aid and non-governmental projects, have frequented headlines and bestseller lists in recent years (e.g. Moyo 2009; Banerjee and Duflo 2011; Karlan and Appel 2011). There has also been a spate of articles and books mounting critiques of the tools traditionally prioritised by policymakers in the measurement of physical, mental and socioeconomic well-being, both at the individual and national scale. Jerven (2013), for example, presents a damming appraisal of the calculation, interpretation and ultimately misuse of African gross domestic product (GDP) statistics. Randall et al. (2011, 2013) highlight the shortcomings of generic large-scale demographic and health surveys in accurately mapping cross-cultural diversity in human residence and resource flows, obscuring true relationships between household structure, health and reproductive behaviours (see also Lawson and Uggla, Chap. 5). Moreover, there is now more recognition than ever before that, if international development policy is to be successful and cost-effective, it needs to be evidence-based, whether that is through randomised control trials or systematic project evaluation (Haynes et al. 2012; Székely 2013; Banerjee and Duflo 2011). Indeed, there is some indication that governments and NGO public policymakers are taking note of the findings in the academic literature. For example, research on the unforeseen impacts of water-tap installation on population change in Ethiopia described in Gibson (Chap. 4) was raised at a recent UK government parliamentary enquiry on Development and Reproductive Health (e.g. Population Action International Report; see Engelman 2006). The potential for rigorous empirical research to influence policy is now apparent, and we believe it is timely for evolutionary anthropologists to demonstrate their contribution.

Finally, stemming from the increased economic pressures placed on universities and other research institutions, funders are increasingly demanding that researchers across the social and natural sciences engage with the applied value and social relevance of their work (e.g. the UK Research Exercise Framework (REF) and Research Councils UK). For example, the 2014 REF, which ultimately determines the allocation of government funding and university league table positions within the UK, required all academic departments to provide case studies of how research has had a direct impact on the wider society. Anthropologists, like all other academics, are being asked to prove their worth.

1.2 Contents of this Book

This edited book is based on a collection of papers presented at a workshop entitled 'Applied Evolutionary Anthropology: Darwinian Approaches to Contemporary World Issues', which we organised at the University of Bristol from 14 to 16 September, 2011. The workshop was funded through generous financial support from the *European Human Behaviour and Evolution Association (EHBEA), the Bio-Social Society* and the *Galton Institute.* The book also represents the first volume in a new EHBEA book series, which aims to showcase the work of researchers exploring evolutionary questions about human behaviour (www.ehbea.com).

Our contributing authors address a wide range of research topics and collectively combine a range of methodologies and sources of data. Each contributed chapter focuses on the integration of evolutionary theory with neighbouring social sciences to yield new and practical insights into major social and health issues of the twenty-first century (e.g. natural resource management, population growth and public health service delivery). In doing so, they demonstrate the potential utility of an evolutionary perspective in the design and evaluation of development and public policy. In addition, each highlights a central feature of evolutionary anthropology, the need to understand human responses to our physical and cultural environment as multidimensional and integrated.

We have divided the book into four parts, each comprising of two to three chapters grouped around an overarching shared theme. This division of themes is somewhat artificial; several key topics and theoretical frameworks are recurrent throughout.

Part 1 '*Development Intervention*' contains three chapters, each concentrating on what evolutionary anthropology has to offer the design of external interventions aimed at improving well-being and/or the mitigation of economic risks in disadvantaged rural communities in the less developed world. Bram Tucker (Chap. 2) tackles the complex topic of agricultural reform, reviewing how key assumptions regarding human rationality have historically played a foundational role in the design and evaluation of large-scale programmes aimed at improving agricultural productivity. Cautioning against the application of a naïve, and ethnographically poorly supported, model of farmers acting to selfishly maximise individual profits, Tucker instead emphasises the importance of collective interests, the propensity for non-selfish behaviour and the avoidance of food insecurity, rather than the prioritisation of profit maximisation. Implications are drawn for the new Alliance for a Green Revolution in Africa (AGRA), with suggested increased focus on community cohesion and the evaluation of wider markers of well-being and equity rather than increases of yield and cash earnings alone. Shakti Lamba (Chap. 3) argues a strong case for convergent evolution between two independent fields addressing the determinants of human cooperation: (1) the academic evolutionary literature, relying mainly on the use of experimental economic games to test hypotheses regarding human cooperative tendencies, and (2) the applied economic literature studying the success and failure of microfinance initiatives, which present 'real world' cooperative dilemmas as loan-group members are liable for debts unpaid by other members. Lamba concludes that in many cases microfinance studies are consistent with the evolutionary literature and its core predictions, but highlights that much uncertainty remains in understanding the mixed success of microfinance programmes. Finally, Mhairi Gibson (Chap. 4) reviews the findings of a long-term study of the impact of labour-saving development project on population change in rural Ethiopia. The chapter reveals a number of unexpected shifts in local demography and health (larger family sizes, poorer child growth and increased outmigration) and parental investment behaviours (greater educational investment) arising as a direct consequence of development intervention. Gibson argues that the findings not only support development policy which favours routinely combining family planning with technological or health intervention, but also reveal the value of an evolutionary approach by providing an explanation of how and why population and health changes may occur.

In Part 2 '*Family Structure and Reproduction*', David Lawson and Caroline Uggla (Chap. 5) consider the theoretical and empirical contribution of evolutionary studies of family structure to the more directly applied literature of population health science. Evolutionary anthropology's emphasis on contextual variation, in both the drivers and impacts of observed diversity of human family structure, is contrasted with the use of large-scale nationally and regionally representative surveys in population health, which often obscure such variation. Focusing on sub-Saharan Africa, shared priorities for future research are highlighted and tentative recommendations made for policy related to topics including fertility decline, the legal status and potential health risks associated with polygynous marriage and the extent to which extended kin can be anticipated to effectively substitute parental care for fostered and orphaned children. The theme of population health is further developed in chapters by Alejandra Núñez-de la Mora, and by Mary Shenk and colleagues. Núñez-de la Mora (Chap. 6) documents a striking variation in breastfeeding rates between first- and second-generation Bangladeshi immigrant populations to the UK. Using concepts from evolutionary life history theory and reproductive ecology, the role of shifting pay-offs to alternative breastfeeding behaviours are discussed. It is argued that declining health benefits and increased opportunity costs to breastfeeding for UK-born women of Bangladeshi origin underlie observed differences. Wider patterns of ethnic and socioeconomic variation in breastfeeding rates are discussed and suggestions made for culturally sensitive maternal and child health promotion programmes. Shenk et al. (Chap. 7) review how evolutionary- and non-evolutionary-minded demographers have approached the topic of biased sex ratios, with particular reference to the strongly male-biased sex ratios common to many regions in South Asia. Novel empirical analyses are presented on the determinants of family-level sex-ratio variation in Matlab, Bangladesh, where, counter to trends across much of the subcontinent, sex ratios have become substantially less male-biased in recent years. Shenk et al. suggest that the utility of evolutionary demography is not that it necessarily improves upon or replaces ideas in the mainstream demographic literature, but rather that it ties disparate concepts and hypotheses together in a broader integrative framework capable of yielding ultimate-level explanations for complex cultural phenomena such as son preference.

Part 3 ‘*Cooperation and Conflict*’ is composed of two chapters that consider the propensity for human violence and punishment. Robert Layton (Chap. 8) reviews influential early philosophical and more current anthropological stances on the extent to which our species should be considered predisposed to violence and aggressive competition in the absence of strong governance. Joanna Bryson and colleagues (Chap. 9) pursue an improved understanding of the puzzling phenomena of ‘antisocial punishment’, that is the tendency to punish those who contribute to the public good, even when those contributions directly benefit the punisher. The authors propose, supported by analysis of cross-cultural economic game data, that antisocial punishment may be best understood as aggressive behaviour directed to perceived out-group members, and that cultural variation in antisocial punishment corresponds to local likelihood that other participants are members of a trusted group. This interpretation identifies a clear need to ensure strong perceptions of mutual trust and shared goals for citizens themselves to respond positively to cooperators and reinforce contributions to public goods.

Part 4 concludes with a consideration of what evolutionary thinking can offer the study of ‘*Health and Diet Behaviours*’. Gillian Pepper and Daniel Nettle (Chap. 10) offer an evolutionary take on the sizeable positive socioeconomic gradients in health behaviour (i.e. activities such as healthy eating and regular exercise) routinely demonstrated in studies of public health. Despite a large volume of research dedicated to the topic, there is still little consensus on the causes of this gradient. Integrating existing explanations at both the proximate and ultimate levels, Pepper and Nettle present a complementary proposal that, as extrinsic risks to mortality increase, the payoffs to investment in preventative health behaviour will decline. They suggest actual and perceived mortality risk should be responsibility modified to encourage increased healthy behaviour for socioeconomically disadvantaged groups. Jonathan Wells (Chap. 11) develops a conceptual model to explain the dual nutritional burden (of under- and over-nutrition) characteristic of many modernising countries. He argues that developmental plasticity which allowed humans to survive challenging environmental shifts over evolutionary history renders some contemporary populations vulnerable to chronic diseases (such as diabetes, hypertension and coronary vascular disease). Wells emphasises the negative effects of global economic forces, particularly the commercial activities of large corporations (via food marketing and distribution), which target 'emerging' economies. Robert Aunger and Valerie Curtis (Chap. 12) also offer a theoretical model. This chapter advocates the value of an 'evo–eco' approach to understanding behavioural change and the mechanisms that underlie it. The model is based around the dynamic relationship between the environment, evolved human cognition and behaviour. They review case studies which reveal how this approach can be used to develop public health and hygiene programmes, for example, in the promotion of hand-washing behaviour.

1.3 What are the Contributions of Applied Evolutionary Anthropology?

Each chapter in this volume makes its own case for the major contributions of evolutionary anthropology, identifying key theoretical, methodological and applied dimensions which may improve human well-being within the contemporary world. In general, three main types of contribution can be distinguished. We briefly outline each below.

1.3.1 Strong Integrative Theory

Evolutionary approaches are led by well-grounded theoretical predictions concerning human motivations, preferences and behaviours. Importantly, this includes a unique consideration of *ultimate causation,* i.e. explanations for behaviour grounded in terms of evolutionary history and adaptive function. Improving our understanding of the evolved design of human body, mind and culture in this way provides a strong predictive and interpretative framework for the study of human susceptibility to conflict, ill health or unhappiness. Indeed, a fundamental observation of evolutionary anthropology is that natural selection has 'designed' the human organism to deploy behaviour which maximises the production of genetic descendants, not health, financial gain or other measures of personal or societal well-being. The chapters in this volume are united in their view that this knowledge has much potential to be of use to the wider society; to help design better interventions, facilitate trade, minimise conflict and to market public health initiatives which improve human well-being (also see Roberts 2011). Furthermore, by embedding *proximate* explanations of behaviour, i.e. those based on the assumed properties of human physiology, psychology or culture, into an ultimate framework, an evolutionary perspective can serve to integrate disparate theoretical frameworks, identifying new links and directing attention to new areas of research. Thus, the integrative nature of evolutionary thinking holds great promise to unify alternative approaches in the social sciences. An anthropological focus complements this unifying potential, assuring that theoretical models are sensitive to the diversity of human history, culture and experience.

1.3.2 Ecological Contingency

One important focus within evolutionary anthropology, of particular relevance to applied studies, is its emphasis on the context dependency of human behaviour. An evolutionary approach argues that huge variation in behaviour exists, because the payoffs to alternative strategies are dependent on local ecology and individual condition, as well as constraints of culture and evolutionary legacy. This standpoint has contributed to an increased recognition in evolutionary sciences that human nature is variable (across both space and time), indicating that findings from one society are very rarely relevant to the wider picture across cultures (e.g. Henrich et al. 2010), and emphasising the value of culturally appropriate methods, data analysis and interpretation. With regard to policy relevance, this perspective supports a long-standing tradition within anthropology, arguing for targeted intervention projects which are designed to address local conditions and specific needs (rather than 'blanket', broad-based initiatives which are applied cross-culturally with little regard to local context).

Additionally, an ecological focus places evolutionary anthropologists in a good position to tackle topics relating to recent changes in lifestyle and physical environment which are having a dramatic impact on human well-being. This includes addressing both how and why humans are likely to respond: for example, by identifying which groups or individuals are likely to be most vulnerable to negative effects of climate change and dietary shifts in transitional economies, or by revealing situations where conflict and social unrest may occur (highlighted in Chaps. 3, 8, 9, 10 and 11 by Lamba, Layton, Bryson, Pepper & Nettle, and Wells).

1.3.3 Mixed Methodologies

AEA builds on a broader disciplinary tradition of applying scientific and social methods and principles to address contemporary world issues. Methodologically, it benefits from the exploitation of mixed methods. It combines scientific rigour (favouring evidence-based research, exploitation of natural experiments and the use of quantitative statistical methods) with contextual detail from anthropology (most notably engaging with ethnographic methods, which draw on in-depth and long-term fieldwork). Increasingly, the complementary collection of qualitative data on local perceptions, attitudes and beliefs provides important detail on the context of human decision-making and behavioural change (see Chaps. 2, 4 and 6 by Tucker, Gibson and Núñez de la Mora,).

1.4 Recommendations

As Monique Borgerhoff Mulder points out in her foreword to this book, transforming loose statements of policy relevance into real impact may present both theoretical and methodological challenges for evolutionary anthropologists. However, in this respect, we are not alone. Balancing applied and pure research remains a long-standing issue in anthropology (and indeed across much of academia) (Sillitoe 2007; Mosse 2013). The chapters in this volume reveal that these challenges may also be the source for new research opportunities for evolutionary anthropologists. To this end, we conclude our introduction with five simple recommendations for evolutionary anthropologists who wish to make their work more applied. These include: (1) directing our research focus towards transitional populations, particularly those most vulnerable to the effects of rapid and recent changes in society and health; (2) improving communication and collaboration with appropriate decision-makers, including national policymakers, research think tanks and non-governmental charities (organisations which can help to guide our research towards the most pressing human issues, but also implement our recommendations); linked to this, (3) disseminating research to a wider audience, through on-line open access reports, presentations to the public and other non-academic publications; (4) using and promoting mixed-methods approaches which demonstrate the value of integrating small-scale anthropological analyses, which reveal the primacy of local context, with the large-scale data sets prioritised by economists and population scientists; and finally, but most importantly, (5) ensuring active consideration of how research insights may improve human welfare, in particular encouraging students and junior researchers to stay well-informed on key public debates. We hope this book itself succeeds in addressing this final recommendation, stimulating further research and teaching as well as inspiring dialogue on topics relating to the application of evolutionary anthropology.

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Part I
Development Intervention

Chapter 2
Rationality and the Green Revolution

Bram Tucker

Abstract Adaptation via differential success among competing individuals creates winners and losers. But adaptation via cultural group selection creates benefits that are shared among group members. During the twentieth century, evolutionary biologists and economists developed parallel theories of rationality, the gene's eye view and rational choice theory, which imagine humans as self-interested individuals maximizing consumption of scarce resources. When rational choice theory was applied to agricultural development in the Green Revolution programs of the 1940s to the 1980s, it turned otherwise cooperative farmers into competitors for cash profits, resulting in a process akin to differential mortality, generating wealth for some but exacerbating poverty for many. I suggest that evolutionary biology may offer an alternative view of human rationality, one consistent with ethnographic evidence of farmers' behavior. One emerging candidate for a "Rationality 2.0" assumes cultural inheritance, cultural group selection, strong reciprocity, and bounded rationality. Farmers make decisions that balance individual benefits with family and community well-being. While the new Alliance for a Green Revolution for Africa (AGRA) seeks technical solutions within its seeds, soils, policy, and markets programs, Rationality 2.0 suggests that AGRA should also promote community cohesion, autonomy, human capability, and reduced dependence on imported technology.

2.1 Introduction

Evolutionary biologists and microeconomists working from a shared background in Enlightenment-era philosophy developed parallel theories of human rationality over the twentieth century. Practitioners of both fields developed a theory of human behavior in which (1) organisms are autonomous individuals (2) who are self-interested, helping others only when helping benefits the helper more than not helping

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would, (3) who compete with other individuals for scarce resources, and (4) who make decisions through optimal cost–benefit calculus. In evolutionary biology, this view of rationality has been termed “the gene’s eye view” (Laland and Brown 2002; Dawkins 1976). It served as the main theory of rationality in human sociobiology and behavioral ecology throughout most of the twentieth century. Economists call their version “rational choice theory.” Born from the utilitarianism of the eighteenth century and formalized during the marginal utility revolution of the late nineteenth century, today it remains the worldview of most business and development economists (Hunt 2002).

As evolutionary scholars ask how we may apply our knowledge to guide conservation and development programs and public policy, it is important that we make our rationality assumptions explicit. Because evolutionary biology shares a theory of rationality with economics, an applied evolutionary science hazards reinventing pro-business development agendas. I argue that evolutionary theory has the potential to offer an alternative concept of rationality, one that leads to more just and effective programs and policies by embracing humanity’s prosocial nature rather than assuming self-interest.

Just as biologists commonly assume that animals adapt to their environments via interindividual competition for fitness, development economists often assume that farmers adapt primarily through interindividual competition for profits. There are at least two problems with this assumption. One problem is that this is violated by descriptive evidence of how humans actually behave. Recent experimental evidence suggests that humans are often altruistic, even in the presence of incentives to be selfish (discussed below; Gintis 2000; Henrich et al. 2005; Herrmann et al. 2008; Marlowe et al. 2008). The ethnographic record depicts farmers as acting as members of cohesive social groups based on kinship and community, with goals of subsistence, social continuity, and the leveling of inequalities, where individualism and profit maximization are viewed as antisocial and immoral (Cancian 1989; Fortes 1953; Foster 1965; Polanyi 1977; Sahlins 1972; Scott 1976; Tucker et al. 2011).

The second problem with assuming adaptation through interindividual competition is that regardless of how well interindividual competition may work to optimize farmers’ productive efficiency, the process of differential success is not very “nice,” for it creates losers as well as winners. If we accept this lack of niceness as inevitable, then we are giving in to the naturalistic fallacy, admitting that because interindividual competition is (supposedly) human nature, then it must be socially just (Frankena 1939). Recent surveys of the political attitudes of evolutionary anthropologists (Lyle and Smith 2012) and evolutionary psychologists (Tybur et al. 2007) find that on average, we value human rights, political compassion, and equitable wealth distribution, suggesting that we may not be willing to accept the human costs of increased inequality in favor of economic growth. I am not arguing that we should disbelieve scientific evidence for the gene’s eye view and rational choice based on our political leanings; I am arguing that there is no good reason to employ these theories in development programs and policies if they do not serve our social justice goals. Evolutionary theory may help us to imagine effective alternatives.

Consider the example of the Green Revolution, a series of large-scale agricultural development programs in the 1940s through 1980s that encouraged farmers throughout the world to intensify cash crop production using high-yielding grain varieties and petrochemical inputs. The Green Revolution attempted to transform socially cohesive, self-sufficient farming communities into individualistic, competitive, market-dependent agricultural entrepreneurs, under the assumption that maximizing yield and market sales is equivalent to reducing poverty. While many agronomists and agricultural economists judge the Green Revolution to have been a great success, responsible for reducing global food prices and increasing national exports (e.g., Singh and Day 1975), in many cases the Green Revolution exacerbated inequality and worsened poverty, as, in a process akin to differential mortality, those who could not afford costly inputs were outcompeted by their more wealthy neighbors (Cleaver 1972; Prahladachar 1983; Wade 1974; Yapa 1993). The Green Revolution also reduced farmers' confidence in their traditional agricultural knowledge (Stone 2007) and polluted the environment (Antle and Pingali 1994; Klemick and Lichtenberg 2008; Meza-Montenegro et al. 2012).

This chapter attempts to use evolutionary theory to envision a new theory of rationality, one that provides a better match to the descriptive evidence for human behavior from experimental studies and ethnography, and that may be more consistent with social justice goals. I begin by reviewing the parallel historical construction of the gene's eye view and rational choice theory. Philosophers refer to these as "normative" theories of rationality, meaning that they use formal logic and mathematics to predict the choices a person ought to make (Elster 1986). I refer to them collectively as "Rationality 1.0." Then, I introduce the Green Revolution as an example of the application of Rationality 1.0 to international development agendas. I contrast this to descriptive evidence of farmers' behavior from the ethnographic record.

Then I offer a "descriptive" theory of rationality, one that works inductively from descriptions of behavior toward general explanation (Elster 1986). While Rationality 2.0 may ultimately take many different forms, a cohesive literature supports one version based on evidence that (1) people make decisions based on socially learned information, (2) group-level traits often have a greater influence on individual welfare than do individual traits, (3) people are helpful even when there are no benefits to being helpful, and (4) reward maximization is less realistic than goal satisfaction. If successful economic development is viewed as a process of group-level cultural adaptation, then benefits are likely to be shared among group members, fostering solidarity rather than inequality.

As the Gates and Ford Foundations launch a new Alliance for a Green Revolution in Africa (AGRA), evolutionary biologists could play an important role in explaining and predicting human behavior. I conclude this essay by discussing how a cooperative adaptive community approach could be orchestrated by AGRA.

2.2 Rationality 1.0

2.2.1 Tenet 1: Decision-Makers are Autonomous Individuals; Group Behaviors are best Understood as the Cumulative Effect of Multiple Individual Decisions and Actions

Elster (1982) refers to this assumption as "methodological individualism"; it asserts both that individuals are motivated primarily by endogenous interests like survival and reproduction rather than exogenous factors like social structure, and that group-level phenomena like herd behavior or social institutions are best studied as accumulated individual decisions and behaviors.

In microeconomic theory, methodological individualism comes from Bentham's utilitarian school of thought (Hunt 2002). Bentham asserted that all men, women, and animals seek pleasures such as advantage, goodness, and happiness, and avoid pains such as mischief, evil, and unhappiness (Broome 1991, p. 1). An analyst can sum this list of "utilities" and subtract the "disutilities" to estimate net utility. Utility analysis gained prominence in the late nineteenth century, as Stanley Jevons, Karl Menger, and Leon Walras attempted to predict the behavior of consumers, leading to such concepts as diminishing marginal utility and the determination of price by supply and demand (Blaug 1962; Hunt 2002). Utilitarian public policy assumes that an economy's success may be evaluated by the cumulative net utility of its members. It is relatively insensitive to social inequality, so long as the cumulative pleasures outweigh cumulative pains (Broome 1991).

In evolutionary theory, methodological individualism is partially the result of the "levels of selection" debate of the 1960s. Ornithologist Wynne Edwards (1962) argued that some birds perform behaviors that increase their individual chances of death for the collective good of population control. Williams (1966) responded that if some individuals within a population possessed an allele that resulted in suicide while others had a mutant allele causing selfishness, those with the suicide allele would be less likely to survive to reproduction. Carriers of selfish alleles would easily outcompete their suicidal cousins, so that group-promoting behavior is unlikely to evolve.

2.2.2 Tenet 2: Individuals are Inherently Self-Interested; an Individual only helps Others when the helpful Behavior Delivers Greater Benefits to that Individual than not Helping Would

By the late nineteenth century, utilitarian economists were modeling the strategies of abstract individuals called firms, consumers, and workers who pursued contradictory goals (Hunt 2002, pp. 248–272). Nevertheless, physicist John Von Neumann and economist Oskar Morgenstern (1944) accused economists of primarily modeling "Robinson Crusoe" economies consisting of individuals acting in isolation. In an explicit effort to help economics "mature" into a more quantitative, rigorous discipline like physics, Von Neumann and Morgenstern developed game theory models that simulated one person's best strategy given the potential options and payoffs faced by others. Depending on the potential payoffs from different courses of action, the number of actors, and the amount of information available, individuals maximized their private returns by either cooperating or refraining from cooperation (defection).

By the 1960s, evolutionary theorists questioned why, given that a carrier of a gene leading to altruism is less likely to survive and reproduce than a selfish individual, we nonetheless see cooperation throughout nature, from bee colonies to flocks of birds to herds of ungulates to human society. W. D. Hamilton (1964) advanced kin selection theory, in which close biological relatives help each other at a cost to themselves when their help promotes the survival and reproduction of fellow carriers of the same genetic material. Trivers (1971) argued that an individual may help someone who is genetically unrelated if the person being helped can reciprocate in the future. More recently, evolutionary anthropologists have argued that an individual may generously help others in exchange for prestige, which may have greater fitness benefits than were foregone in the act of charity (Hawkes & Bliege, Bird 2002).

Evolutionary biologists used game theory to extrapolate the consequences of interactions among individuals with divergent interests. In evolutionary game theory, a population of players with different strategies interact repeatedly over a series of rounds, where the "points" an individual scores in round x become descendants inheriting the same strategy in round x+1, thus simulating selection. The frequency of individuals practicing each strategy changes over rounds, with some going extinct while others proliferate, until eventually, no more change is possible as each strategy holds the others in check. Among the lessons learned from evolutionary game theory is that cooperative strategies may outcompete selfish ones when there is an additional cost to defection, such as players withholding cooperation with those who defected against them in the previous round (Axelrod and Hamilton 1981).

2.2.3 Tenet 3: Individuals Compete for Scarce Resources

Thomas Malthus' (1888) famous argument that humans reproduce at a faster rate than the increase in food supply is cited in the literatures of both fields. Economists and evolutionary biologists argue that individuals gain competitive advantage by increasing the efficiency with which they procure limited resources and convert them to value.

Economists refer to the processes by which human labor turns natural resources into consumable goods as "production," which corresponds to foraging and feeding in biology. In agricultural economics, a farmer spends labor, cash, land, fertilizer, and pesticide and gains a harvest of grain, tubers, pulse, or other products, which the farmer then converts into utility through consumption (in the household) and exchange (in the market; Ellis 1988; Sadoulet and DeJanvry 1995). In behavioral ecology, specifically optimal foraging theory, foragers spend time and energy to gain food energy and convert the energy into fitness through consumption and sharing with kin and others who are likely to return the favor (Stephens and Krebs 1986). Efficient behaviors are those with high production of either cash (and utility) or energy (and fitness), net of labor and other costs.

Development economists have traditionally viewed poverty as a result of resource scarcity or inefficient production and marketing behaviors (e.g., Sachs et al. 2004; FAO 2009). Poverty reduction programs often attempt to increase the efficiency of production and exchange by increasing gross gains with technological innovations while reducing costs through donations, credit, and infrastructural improvements.

2.2.4 Tenet 4: People make Decisions Through a Computational Weighing of Costs and Benefits, Akin to Optimization in Infinitesimal Calculus

If individuals win utility and fitness competitions through self-interest and efficiency, then decisions are basically like optimization problems in calculus. Economists and biologists habitually speak of individuals attempting to “maximize” utility or fitness through their choice of actions.

Some scholars hold that maximization is only a handy simplifying assumption to make modeling easier, and not a descriptive account of how the mind actually generates judgments. They argue that individuals who habitually choose courses of action that result in a greater fitness payoffs leave more descendants, so regardless of how the mind works at cognitive level (or how the brain works at a neurological level), the outcome of thought processes should approximate the outcome of optimality models, whereas the latter have the benefit of analytical parsimony (Elster 1986; Foley 1985; Smith and Winterhalder 1992). By contrast, other scholars argue that the brain actually maximizes firing of pleasure-inducing neurons in the cerebral cortex (Padoa-Schioppa and Assad 2006; Knutson and Peterson 2005).

2.3 Rationality 1.0 Applied: The Green Revolution

2.3.1 Overview

The Green Revolution started when agronomists and agricultural economists motivated by Malthusian concerns established the International Maize and Wheat Improvement Center (*Centro Internacional de Mejoramiento de Maiz y Trigo*, CIMMYT) with funding from the Rockefeller Foundation in 1943. The CIMMYT promoted intensive cultivation of high-yielding varieties of maize and wheat in Mexico. In the 1960s, the Ford Foundation working with the government of India introduced CIMMYT wheat to farmers in the famine-stricken Punjab region, while the Ford and Rockefeller Foundations co-funded the creation of the International Rice Research Institute (IRRI) that distributed hybrid rice throughout Southeast Asia. On paper, the primary objective was to provide hybrid maize, wheat, and rice varieties that provided greater outputs with less investment of labor (de Gregori 2004). In practice, these hybrid grains came as part of a package that included intensive farming techniques like plow agriculture and monocropping, encouragement to use chemical fertilizers, pesticides, and herbicides, and a business plan, sometimes including actual business training, for the marketing of cash crops (Cleaver 1972; Wade 1974).

The Green Revolution projects exemplified Rationality 1.0 for the reasons discussed in next three sections.

2.3.2 Assumption 1: The Basic Units of farm Decision-Making are Individuals and Households, who Compete to Maximize Yields; thus, Farmers Adopt new Agricultural Technologies once they Witness Superior Production, and Traditional Common Property Resource Management Schemes are Inefficient

As Evenson and Gollin (2003, p. 758) say, “When a farmer chooses to adopt a new variety to replace an older variety, it reflects the farmer’s judgment that the new variety offers some net benefit or advantage.” This is the basic assumption in Ryan and Gross’ (1943) innovation diffusion model, which holds that farmers will adopt a new crop or technology once they have witnessed its superior benefits (see also Rogers 2003). It assumes that each individual is free to make her own choice; that individuals want to produce more, even when this means outproducing their neighbors; and that late adopters and non-adopters are “laggards” who lack sufficient information. Interestingly, Yapa (1993) interviewed supposed Green Revolution “laggards” in Karnataka, India, and found that they were generally quite knowledgeable about new maize varieties, but preferred traditional farming for “what appeared to be very rational reasons” (Yapa 1993, p. 258).

Green Revolutionaries tended to distrust common property management institutions because of widespread faith in Hardin’s (1968) infamous “tragedy of the commons” argument, which holds that selfish individuals will overexploit common property when private gains outweigh public costs. Thus, agricultural development agents sought to replace institutions like Bali’s system of water temples with private property (Lansing 1991), an example I discuss in greater detail below.

2.3.3 *Assumption 2: Farmers are Profit-Motivated Cost–Benefit Accountants and Nascent Businessmen*

Cleaver (1972, p. 179) reports that the president of the Rockefeller-funded Agricultural Development Council Arthur T. Mosher, “harps repeatedly on the theme of teaching peasants to want more for themselves, to abandon collective habits, and to get on with the ‘business’ of farming.” Mosher encouraged agricultural extension classes in which farmers were taught the value of earning, saving, and spending money.

Jones (2005) argues that development economists typically treat cultural traditions and institutions as patriarchal, corrupt, and authoritarian, as barriers to individual liberty and rational thought. Reducing the power of traditional culture allows the farmer to realize his natural, rational potential. As Singh and Day (1975, p. 683) conclude from a study of the Green Revolution in Punjab, “…in spite of vast institutional differences distinguishing them [Indian farmers] from their counterparts elsewhere [agri-businessmen], peasant farmers are amenable to economic incentives and respond rationally once appropriate account is taken of the decision milieu.”

2.3.4 *Assumption 3: The main Problem Facing Farmers is Scarce Agricultural Production due to Inefficient Technologies*

This perspective sees farmers’ poverty as resulting from their technological primitiveness, ignoring histories of colonial invasion and domination that first created the peasantry as a rural underclass (Wolf 1957). Scarcity was defined in strictly Euro-American terms, as low production per unit land and low investment of mechanical and chemical inputs (Singh and Day 1975), coupled with “missing markets,” the failure to buy and sell production and labor (de Janvry et al. 1991). Meanwhile, Yapa (1993) argues that the Green Revolution actually created scarcity, by promoting technology that requires scarce inputs, degrading natural ecological relationships thus engendering greater need for scarce inputs, encouraging cultural concepts of market success and consumption, and a replacement of common traditional agricultural knowledge with academic knowledge available only from experts (Fig. 2.1).

2.3.5 *Green Revolution Outcomes*

Those who see the Green Revolution as a success point to increased national grain production and exportation, increased cash incomes of farmers, increased use of tractors and fertilizer with a concomitant decrease in human and animal labor, increased use of modern technology, and lower global food prices (de Gregori 2004;

Fig. 2.1 A farmer in Central Malawi applies chemical fertilizer to hybrid, irrigated maize. The government of Malawi issues fertilizer coupons to farmers to encourage them to use Green Revolution technologies. (Photo by Joseph Lanning)

Evenson and Gollin 2003; Murgai et al. 2001; Singh and Day 1975). Detractors argue that increases in agricultural production were illusory, for monocropping dwarf varieties without fallow facilitates the spread of pests and crop diseases thus requiring the farmer to purchase increasing quantities of inputs (Lansing 1991; Yapa 1993). Chemical fertilizers, pesticides, and herbicides, as well as diesel fuel for agricultural machinery, generated pollution, which diminished human health and long-term soil quality (Antle and Pingali 1994; Meza-Montenegro et al. 2012), and killed aquatic animals that perform important ecological functions and are part of the food supply (Klemick and Lichtenberg 2008). Among the first outcomes of the Green Revolution was that national and international grain markets were flooded, resulting in reduced purchase prices and lower profits for farmers, leaving many to wonder whether it was worth the extra effort. Meanwhile, labor-saving technology contributed to a rise in rural to urban migration and concomitant large-scale unemployment (Wade 1974, p. 1095). Certainly, the Green Revolution created or reinforced dependence on the market, and particularly on international agribusiness, as a source for purchased inputs and as a buyer of grain (Cleaver 1972, p. 179). Stone (2007) has argued that this dependence on seed companies resulted in farmer “deskilling,” as farmers’ traditional agricultural knowledge was replaced with blind faith in seed companies. Others have worried that this dependence on seed companies eroded agrobiodiversity (Harlan 1975; but see Brush 1992), and replaced government control of agrarian policy with control by agribusiness (Nanda 1995; Stone 2007).

By assuming that farmers are nascent businessmen, Green Revolutionaries recreated the peasantry after their own image. They created an environment of individual competition, in which a process akin to differential survival and reproduction saw the acceleration of the profits of those who could afford pesticides, herbicides, diesel, and machinery, with increasing poverty for those who were selected against (Cleaver 1972; Freebairn 1995; Junankar 1975; Prahladachar 1983). At a national scale, regions that received Green Revolution interventions outcompeted those that did not, generating regional inequalities (Cleaver 1972).

2.4 Ethnography as Descriptive Evidence for Rationality

2.4.1 Tenet 1: Rural Peoples Self-Organize into Strongly Cohesive Social Units that Constrain and Sometimes Determine Individuals' Choices

The ethnographic record provides a rich descriptive account of farmers' choices and strategies before and during the changes wrought by the Green Revolution. Ethnographers have found that in many rural societies, people divide themselves into cohesive groups like ethnicities, tribes, lineages, clans, phratries, moieties, age-sets, and offices (Bohannan and Middleton 1968). While many such groups are organized by kinship, most ethnoclassifications of kin exclude some genetic kin and include genetic nonrelatives, while weighing kinship proximity differently than would Hamilton's coefficient of relatedness (Beattie 1964; Sahlins 1976).

Writing about unilineal descent groups (matrilineal and patrilineal lineages and clans) in Africa, Fortes (1953) argued that such groups are corporate, meaning that they act as one body to achieve social and material goals. Far from being autonomous individuals, persons are "an assemblage of statuses" (Fortes 1953, p. 37). A man is a father to some, an uncle to others, an elder or junior, a clan-mate or age-mate to still others. Each of these statuses is associated with a set of expected behaviors that dictate, or at least severely limit, the choices that a man can makes. This system of expectations constitutes law and morality. The severity of crimes and other deviant behaviors depends on the structural position of the plaintiff and defendant. It may be moral to kill an enemy, while killing a clan-mate necessitates a bloodwealth payment of cattle to the grieving family, and killing a parent, sibling, or child is punishable by death. Traditionally, it is often the descent group rather than the individual that owns property. Fortes argues that the major function of descent groups is to organize resources for reproduction and survival so as to perpetuate the clan for eternity. Within this system, individuals see themselves as acting in favor of a grand, intergenerational program rather than pursuing self-interest.

2.4.2 Tenet 2: Much Economic Behavior Outside of Capitalism Functions to Reinforce the Solidarity of Social Groups, Making Individualism and Profit-Seeking Antisocial and Immoral

In his famous *Essai sur la Don*, French sociologist Marcel Mauss (1925) attempts to understand why in many traditional societies, wealth is generated by giving valuables away to others rather than by possession. In Melanesia, elite men undertake dangerous sailing adventures in order to gift shell artifacts to counterparts on neighboring islands, while on the Pacific Northwest Coast of Native North America chiefs host Potlatch parties in which they give all their possessions away to their guests. Mauss concludes that the function of exchange is sociality itself. As one of Richard Lee's (2003, p. 119) Kalahari San informants said of hxaro gift exchange, "we don't trade with things; we trade with people!" In noncapitalist economies, argues Karl Polanyi (1977), reciprocal exchange builds an egalitarian social order while redistribution builds hierarchical social order. Exchange in capitalism, by contrast, contributes to individual benefits rather than social goals.

In societies where exchange is performed primarily to cement social ties and fulfill moral obligations, maximizing profit is tantamount to cheating the social order. And so Christians, Jews, and Muslims have traditionally considered usury and avarice to be sins. Foster (1965) argues that many peasants suffer from "an image of limited good," which leads them to suspect that those who experience better-than-average financial or agricultural successes, due to hard work or chance, have stolen more than their fair share of the limited good. Likewise, Azande of Sudan and many other peoples believe that differential success implies that one has cheated the social order by witchcraft or sorcery (Evans Pritchard 1937). Shipton (1989) describes the case of Luo farmers in Kenya, among whom profits from a certain class of antisocial activities results in "bitter money," funds that, if spent, will lead to ruin. These antisocial activities include theft and windfalls (since the Luo have Foster's image of limited good), as well as profits from selling land (traditionally a lineage asset), roosters (a symbol of male fertility and lineage continuity), mining gold (from underground, realm of ancestors), and selling tobacco and marijuana (where smoke is symbolic of ancestral spirits). Bitter money can be converted to a safer form in a ceremony in which much of the money is given away to members of the community. Cancian (1989) describes how successful farmers in Mexico are expected to volunteer for a cargo office, the primary role of which is to fund expensive public festivals that essentially redistribute the successful farmer's wealth. Individuals who decide to adopt a self-interested business persona place themselves at risk of being accused of antisocial or immoral behavior.

2.4.3 Tenet 3: There are Ecologically "Adaptive" Benefits for Strong Social Cohesion in Agricultural Communities

I place "adaptive" in quotes because I am using the term as would a cultural ecologist rather than a Darwinist, to refer to a population's fit to its resource base. Among the resource challenges that all farmers face are periodic and unpredictable shortages of food and labor. A benefit of cohesive social groups is the facility of food and labor sharing. Traditional work-sharing institutions meet labor needs that are not easily satisfied by either the household's own labor supply or by markets and self-interest. Social cohesion may discourage free riding and common property tragedies. For example, farmers in the Swiss Alps work communally to create and maintain common property irrigation channels and to clear upland pastures (Netting 1981). Rice cultivators in the Amazon basin, like many Latin American farmers, sponsor festive work parties and reciprocal labor exchange groups to accomplish seasonal labor-intensive tasks like clearing, weeding, and harvesting (Chibnik 1994). Because such

Fig. 2.2 Green revolution technologies have not arrived in Madagascar's rural southwest, where this Vezo–Mikea man applies labor and no other inputs to his swidden sweet potato field. (Photo by Bram Tucker)

tasks are seasonal, all farmers within a community face increased labor needs simultaneously; hiring labor is prohibitively costly due to high demand and low supply. Work parties and exchange labor groups are more efficient than hired labor in the context of trust (Fig. 2.2).

2.4.4 Tenet 4: Peasant Farmers may be less Concerned About Scarcity than are Economists

Sahlins (1972) argues that utility maximization is a cultural construct associated with capitalism's culture of consumption. In noncapitalist societies, people may enjoy a state of "original affluence" in which their limited wants are easily satisfied by meager means. Scott (1967) applies a similar argument to farmers in Southeast Asia, although the farmers he portrays are far from affluent. Citing the "safety first" model of risk minimization, Scott argues that peasants satisfy food security rather than maximizing profit, and that this keeps peasants focused on internal politics. Interestingly, when I ask Masikoro farmers, Mikea hunter-gatherers, and Vezo fishermen in southwestern Madagascar to define poverty and wealth in 16 sex-segregated focus groups, no one mentioned scarcity of resources or inefficient harvesting technologies; rather, they emphasized political barriers to accessing the basic resources needed for livelihood (*velomampò,* what enlivens the heart), resulting in an inability to produce people through biological reproduction, socialization, and ritual inclusion into clans (Tucker et al. 2011).

2.4.5 When the Green Revolution Collides with Traditional Farmers

One of the best case studies of Green Revolution programs clashing with traditional social organization comes from Lansing's (1991) description of highland Bali. In the 1960s, the IRRI introduced high-yielding rice to Balinese farmers. Farmers were encouraged to maximize production by replacing fallow periods with fertilizer, and by consolidating rice paddies to facilitate machine tilling. While yields increased over the first few years of the new program, they soon diminished precipitously as pest populations exploded. To combat pests, extension agents encouraged farmers to purchase pesticides, greatly diminishing the net benefits of Green Revolution methods.

The Green Revolution failed in highland Bali because agricultural extension workers disregarded the traditional social institutions that managed Bali's intricate island-wide irrigation network. At each node in the irrigation system stands a temple, attended by a priest (Fig. 2.3). There is a hierarchy of priests corresponding to the hierarchy of irrigation nodes, with the main priest or *Jero Gde* serving the largest water temples at the sources, the volcanic crater lakes near the mountain summits. Together, the priests manage water flow so that farmers upstream and downstream receive equitable amounts of water. They synchronize harvest throughout the island, which reduces pests by seasonally denying them crops upon which to feed. Despite the reliance on common property, there is no tragedy of the commons. The *Jero Gde* cooperates with priests downstream because failure to do so risks angering of the Mountain Goddess who could dry out the whole system. Priests and farmers downstream cooperate because they believe that they require the blessings of priests upstream, especially in the form of special holy waters that are carried from the crater lakes to anoint each individual field. Largely thanks to Lansing's research, agricultural policy in Bali has shifted to supporting the water temple system, and rice yields have rebounded.

Another example of farmers' traditions clashing in Green Revolution assumptions of rationality is reported by Clawson and Hoy (1979) from the Mexican village of Nealtican, where farmers consistently rejected attempts by CIMMYT to introduce hybrid maize for cultural and adaptive reasons. Nealticanos rejected hybrid maize and intensive cultivation in part due to their practice of partible inheritance of land. On a farmer's death, his land is divided into equal shares among all his male and female offspring, where each share is equal in terms of land quality rather than size. While CIMMYT viewed the resulting scattering of small fields to be irrational, farmers understood the adaptive benefits. Each plot is planted with the best suite of crops for given soil, drainage, and solar conditions, and scattered fields mitigate the risks of crop failure.[1]

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[1] A reviewer commented on the similarity of farmer's prosocial behavior and the political philosophy of communism. While this comparison has been made before (e.g., Lee 1990), I believe this to be a semantic issue. The word "communism" to most people refers to state-sponsored communism, which, as I address in the conclusion, has historically failed when applied to agriculture. Farmer's social organization would be a more organic form of socialism.

Fig. 2.3 Water temple priests in highland Bali preparing ritual offerings at the site of one of the nodes in the island-wide irrigation network. The traditional system of water temples effectively manages access to water and controls pests without the need for Green Revolution technologies. (Photo by J. Stephen Lansing)

2.5 Toward Rationality 2.0: One Possible Approach

2.5.1 Overview

Recent literature in theoretical biology and evolutionary anthropology provides some intriguing alternatives to the central assumptions of Rationality 1.0. While practitioners of these fields are not in agreement about what form Rationality 2.0 will take, I present one possible version based on social learning, cultural group selection, strong reciprocity, and bounded rationality. Scholars hotly debate concepts like cultural inheritance (Boyd et al. 2011 versus Lehmann et al. 2008), multilevel selection (Wilson and Wilson 2007 versus West et al. 2011), and interpretations of experimental game results (see Henrich et al. 2005 versus Hagen and Hammerstein 2006), so I will balance enthusiasm for this version of Rationality 2.0 with a brief summary of critiques.

2.5.2 Tenet 1: Humans make Decisions as Individuals and *as Members of Groups*

Methodological individualism implies that behavior is the result of individuals' judgments and choices. Yet research from behavioral psychology suggests that much of animal and human behavior involves learning from the behavior of others (Zentall and Galef 1988). Boyd and Richerson (1988) argue that while individual judgment requires information and time and offers few guarantees of success, imitation is fast, easy, and likely to be successful, at least when neighbors are likely to be well adapted. So a diner in an unfamiliar restaurant may find it easier to order whatever seems popular rather than scrutinizing the menu, while pedestrians cross streets when others do, rather than looking at traffic and signs. Social learning permits cultural inheritance and the nongenetic evolution of human social behavior (Richerson and Boyd 2005).

Individuals are almost never completely autonomous. As you read these words, you face literally thousands of behavioral options: You could set this paper alight, you could eat it, you could put it on your pet's head, you could throw yourself bodily from the nearest window, etc. Most sane readers will do none of these behaviors, even if some happen to yield great personal benefits, because society deems these acts to be abnormal. People punish those who act abnormally and reward those who act in a normal or moral way. At this moment, you face very few "normal" options: You could continue reading, or take a coffee break (unless you are a devout Seventh Day Adventist, or are pregnant, in which case you may be chastised for drinking coffee). Boyd and Richerson (1992) demonstrated that in an N-person iterated prisoner's dilemma game, a small number of "moralistic punishers," who punish both defectors and other players who fail to punish defectors, can stabilize cooperation in a large population. Moralistic punishers pay the costs of creating a public good (cooperation) for which non-punishers free ride. But they survive at stable numbers within the population because the population, and they as members of it, does better when they enforce cooperation.

It is tempting to conclude that imitative social learning and adherence to social norms eliminates all agency from human decision-makers, rendering them passive social puppets, as some social theorists have argued (de Munck 2000). Several scholars have argued against this interpretation (Stone 2007; Sperber and Claidière 2008; Tucker 2012). Among humans, all individual learning involves social learning because perception is colored by socially learned cultural and linguistic categories (Ross 2004). Simultaneously, despite a penchant for imitative behavior (Horner and Whiten 2005), much social learning involves individual judgments about whom to copy. In a study of the determinants of risk and time preferences among farmers, foragers, and fishermen in southwestern Madagascar, I concluded that social conformity and individual costs and benefits co-influence their choices (Tucker 2012). The safest conclusion is that people make decisions as both individuals and as members of groups.

2.5.3 Tenet 2: Common Group Behaviors may have a Greater Influence on one's Fitness than one's Individual Choices

Evolutionary biologists have long rejected group selection because individuals who sacrifice themselves for the good of the group are less likely to reproduce. Yet, group selection can function when interindividual fitness differences are swamped by intergroup fitness benefits. For example, if mutual cooperation is more beneficial than defection, then populations containing the moralistic punishers described above (Boyd & Richerson 1992) will outcompete those who lack them. This creates a benefit for all members of the population including the moralistic punishers, which keeps the moralist punishers from going extinct.

Boyd and Richerson (2010) have argued that group selection is especially likely with the inheritance of nongenetic cultural information. Humans face a number of survival challenges for which there are multiple cultural solutions. For example, people adapt to seasonal cold with a range of clothing styles, all of which are similarly functional. But only a small range of clothing styles may become “normal” within a particular community, perhaps the style worn by prestigious or successful individuals, or whatever style happens to emerge as most common as people copy each other randomly. McElreath et al. (2003) have suggested that people use these fitness-arbitrary norms to identify others that are likely to share the same cooperative norms. An Inuit wearing a parka just like yours is likely to share your concepts of morality and fairness (thus solving “coordination problems”). Thus, we have a natural tendency toward what evolutionary biologists would call multiple stable equilibria among demes, or what social scientists call within-group solidarity and between-group exclusion. Under such conditions, common group behaviors may have a larger influence on one’s fitness than one’s individual choices and behaviors.

While some consider group selection to be a different kind of evolutionary force (Wilson & Wilson 2007; Boyd and Richerson 2010), West et al. (2011) argue that group selection is simply kin selection among individuals from a different point of view. Models by George Price (1970, 1972) demonstrate that kin selection and group selection are mathematically indistinguishable. West et al. (2011) argue that the small groups that enforce cooperation through group selection are necessarily closely related, whereas Boyd and Richerson (2010) argue that group selection acting on cultural traits can enforce cooperation on a large scale, among unrelated individuals. It is beyond the scope of this review to settle this debate, but it is worth noting that even the critics often find group selection to be a useful concept, if only as an alternative way of describing selection among individuals (West et al. 2008).

2.5.4 Tenet 3: People are Often nice when there is no Calculable Advantage to being nice

This is called Strong Reciprocity (Gintis 2000). It is predicted by the theories summarized above: Societies enforce norms for what constitutes niceness, generosity, fairness, selflessness, etc.; children are trained from a young age to expect praise for conforming to norms and punishment for deviating them, and that praise and punishment comes from other people as well as supernatural beings (Atran and Henrich 2010); societies that promote niceness generate benefits shared by all members, even those whose individual interests are sometimes sacrificed as a result of their prosocial acts.

Proponents of strong reciprocity find support for their views in the results of behavioral game experiments. Give someone US$ 10 and ask her to give any portion of it to a random stranger. A utility-maximizing individual should keep all US$ 10. But when this “Dictator Game” is played around the world, players typically give something, often half (for equity is a common norm of fairness). In the Ultimatum Game, player 2 can choose to either accept player 1’s donation or reject it, where rejection means that neither player keeps any of the money. Ultimatum game experiments demonstrate that people will punish those who make unfair or stingy offers, even at a cost to themselves (Henrich et al. 2005); indeed, they do so even if the offer deviates from the norm by being overly generous (Herrmann et al. 2008), or if they are a third party to the transaction (Marlowe et al. 2008).

As intriguing as these results are, they are far from unambiguous. Experiments are abstract exercises; they are purposefully so, to control for as many external variables as possible. Yet, this introduces questions of external validity (Does the experiment predict real life? Smith 2005); and internal validity (Do all subjects respond to experiments similarly, or is some of the variation in game play due to variation in understanding of what the game is about? Hagen and Hammerstein 2006). Ethnographic tests of both external validity (Gurven and Winking 2008; Wiessner 2009) and internal validity (Gerkey 2013) cast some doubt on both. Binmore (2005) has argued that even a strategic, self-interested utility maximizer might behave as these experiments demonstrate, especially if the experiment were extended beyond a one-shot choice.

2.5.5 *Tenet 4: The Human mind is Unlikely to Generate the same Judgments as Optimal Calculus*

Beginning in the 1950s (Allais 1953; Simon 1957), some economists and psychologists have tested whether humans behave consistently with Von Neumann and Morgenstern’s (1944) and Luce and Raiffa’s (1957) axioms of stable preferences, dominance, completeness, continuity, invariance, and transitivity. Evidence from risk and time preference experiments largely invalidates rational choice axioms. Humans tend to judge options differently depending on whether stakes are gains versus losses, how options are framed, the size of potential stakes, whether stakes represent money or health, etc. Human judgment deviates from formal logic and statistical analyses in predictable ways that the literature calls “biases”: We overestimate the probability of extreme events, generalize from small samples, perceive illusory cause and effect relationships, ignore potentially significant information, etc. (see chapters in Kahneman and Tversky 2000).

Gigerenzer et al. (2000) argue that cognitive processes are generally classificatory rather than quantitative. Statistical forecasting is a costly thing for a mind to do, for it requires accurate observation, recall of a large sample of observations, and time-intensive mental calculus. A more “fast and frugal” approach is to follow simple rules of thumb, or heuristics. For example, if someone must choose between two options about which there is sketchy information, a simple solution is to choose the option that has more positive information (this is called the "take the best" heuristic). This means that biases and other apparent "errors" in human judgment may actually represent mental shortcuts that are adaptive because they reach a good solution most of the time. This also means that the human mind is unlikely to maximize anything; indeed, a classificatory cognition system is more consistent with "satisficing," achieving basic goals (Simon 1957). Behavioral ecologists have long made similar assumptions that, for example, animals seek risk when hungry but avoid risk when full (Stephens 1981; Hutchinson and Gigerenzer 2005).

2.6 Synthesis and Application

The descriptive evidence from ethnography and the version of Rationality 2.0 presented here provides an alternative to the typical rational choice model common in development economics. Consistent with cultural inheritance theories, farmers culturally adapt to new challenges through a combination of conformity to group-level norms and individual choices. Consistent with cultural group selection and strong reciprocity, farmers form corporate groups like moieties, phratries, lineages, and clans, which provide individuals with their personhood (as "an assemblage of statuses") and define norms of fairness, generosity, and obligation that constitute a code of law and morality. The purpose of descent groups is to perpetuate themselves, so by being born into such a group one enjoys group-level reproductive and survival benefits (i.e., the clan provides access to farmland and facilitates marriage and child socialization), while sacrificing individual autonomy. Within such social structures individuals are not likely to perceive their choices as optimization under scarcity, but rather, as choosing the best among the few normal options to ensure food supply and the production of people.

The first Green Revolution may have brought about a cultural adaptation to a new market niche, but it did so by pitting farmers against each other, by encouraging differential economic mortality. This adaptation benefited the winners, hurt the losers, exacerbated inequality, and encouraged the spread of selfish norms.

Now imagine an alternative Green Revolution crafted around Rationality 2.0, which assumes people are naturally group-oriented, strongly social, and seek safety and continuity (social and biological) rather than profit. As with the first Green Revolution, development practitioners could introduce improved farming methods for increasing yield, and new market opportunities. However, the project should also work with rural communities to strengthen existing social institutions of family, governance, reciprocity, and redistribution, what development economists call social capital (Woolcock 1998) and community empowerment (Binswanger 2007). To limit within-community competition, planners should avoid creating scarcity as Yapa (1993) describes; they should avoid fostering dependence on limited resources from the outside, like seed, petrochemical inputs, and expertise. This suggests a greener Green Revolution, one that favors locally produced solutions like manure fertilizers, compost, and multi-cropping nitrogen-fixing legumes, erosion-reducing shade trees, natural pest deterrents, and local knowledge. Improved seed could be part of the equation, as long as the seed is freely available and has nonmarket as well as market value; it must be edible, able to be replanted, and modifiable by cross-breeding by innovative farmers. Markets can be an important part of the equation, as long as they serve to increase farmers' options of what to do with their crops, rather than creating dependency.

This strongly social vision of development should not be confused as an endorsement of state-sponsored socialism. As Netting (1993) argues, agricultural reform in the Soviet Union and China, which involved state-run collective farms, experienced some of the same maladaptations as plague agribusiness, because both involve a few bureaucrats making decisions for a large land area. Collective agriculture and corporate agribusiness assume that there are economies of scale in agriculture, whereas Netting's evidence demonstrates that smaller farmers produce more food per unit land and other inputs than do larger farms. This is because farmers on small farms are more capable of responding to variations in soil quality and drainage, are more likely to practice labor-intensive, risk-reducing strategies like mounding and irrigation, and are more likely to plan for long-term sustainability since their land is their wealth, to be bequeathed to future generations. I join Netting in arguing that farmers should be granted the freedom to farm on whatever scale they find most "adaptive" in the cultural ecology sense (beneficial given ecological constraints).

Thus, my proposal is commensurate with a rights-based approach to development, in which individuals and communities must be free to make their own cultural and agricultural decisions. Sen (1983, 2000) argues that development agencies may facilitate a rights-based approach by investing in human capability, which refers to an individual's ability to pursue life and livelihoods. Market dependence, excessive taxation, excessive policing, war, infringement of basic human rights, and lack of healthcare, education, and transportation infrastructure may all hinder capability.

AGRA appears to be largely focused on finding technical solutions. AGRA runs four main programs, devoted to seeds, soils, market access, and policy and partnerships (Blaustein 2008; AGRA 2008, 2009, 2010, 2011). Among AGRA's initiatives that fit well with my recommendations are investment in the training of African scientists, which should reduce competition for scarce knowledge; and the creation of local seed, fertilizer, and pesticide companies, which may reduce competition for imported inputs. However, there is almost no discussion in AGRA's documents about farmer's culture or social institutions, and the focus of the program remains cash cropping-improved varieties. I offer AGRA planners two recommendations. First, I suggest that they add to their programs of seeds, soils, markets, and policy partnerships an additional program focused on community, which should be staffed primarily by farmers themselves. Second, I suggest that if the true goal of AGRA is to improve the quality of life for farmers, then they should avoid measuring the success of their programs by increases of yield and cash earnings. Instead, the success of AGRA programs should be judged according to farmers' food insecurity, well-being, empowerment, and equity.

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Chapter 3
A Comparison of the Economic Literature on Microfinance and the Evolutionary Literature on Cooperation

Shakti Lamba

Abstract Microfinance initiatives provide financial support and loans to individuals from low-income backgrounds who are otherwise excluded from mainstream banking services. They do so by providing loans to groups of individuals who are jointly liable for their repayment. This model of lending creates a cooperative dilemma because if any member of a loan group defects and does not repay his/her share of the loan, the other members of the group are liable to repay it for him/her. Maintaining cooperation among borrowers and solving the cooperative dilemma created by the microfinance model may be crucial to ensure loan repayment. A vast literature in economics identifies factors that encourage successful loan repayment in microfinance initiatives and those that prevent defaults. Here, I compare the economic literature on microfinance and the equally prolific evolutionary literature on factors that encourage and maintain cooperation among individuals. I identify parallels between these two bodies of research, which have so far developed independently. Bringing them together enables us to examine the power and limitations of applying evolutionary theory to contemporary economic issues and may stimulate novel questions and insights in both disciplines.

3.1 Introduction

Ever since I first started working on the evolution of cooperation in humans, I have repeatedly encountered questions about how effective evolutionary theory is at explaining behaviour in the real world. Some people ask how any of this research is relevant and useful to society. Stricken both by these academically interesting questions as well as a sense of obligation to taxpayers who fund most scientific initiatives, I have spent some time thinking about them. In what follows, I make a first attempt to address both these questions.

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The broad aim of this chapter is to compare findings from the evolutionary literature on cooperation and the economic literature on microfinance. In Sect. 3.1.3, I explain why I focus on microfinance in particular. I describe what microfinance is, why it is important, how successful it has been across the world and how it might link to evolutionary theory on cooperation. In Sect. 3.2 and 3.3, I review findings from the evolutionary literature on cooperation and the economic literature on microfinance respectively; neither of these is an exhaustive review but rather a targeted summary of key results. To conclude, in Sect. 3.4, I evaluate how the findings of these two independent disciplines compare and whether they might inform each other.

3.1.1 What is Microfinance and What are its Aims?

Microfinance refers to informal and formal arrangements offering financial services to those who are otherwise excluded from mainstream banking services (Brau and Woller 2004). Microfinance providers range from local moneylenders to formal institutions that offer financial services to individuals from low-income households. The full range of services offered by microfinance institutions (MFIs) includes loans (also known as microcredit), savings and insurance schemes (Brau and Woller 2004). However, the major focus of most MFIs is to provide loans. It is this sector of the MFI industry that I focus on in this chapter.

The MFI movement first took hold in Bangladesh led by Muhammad Yunus in the 1970s. With help from the Government of Bangladesh, Yunus established the Grameen Bank in 1976. The aim of the movement is poverty alleviation (Brau and Woller 2004). By providing financial services to individuals from low-income households who otherwise do not have access to mainstream banking services, the long-term goal of many MFIs is to make these individuals economically self-sufficient. However, in the short term, MFIs also offer individuals loans to meet personal expenses such as in the event of emergencies or even weddings. Microfinance is currently one of the most powerful tools available to address poverty as it offers individuals the prospect of economic self-sufficiency rather than temporary aid and caters to people who cannot generate the collateral necessary to access mainstream banking services.

3.1.2 Have MFIs been Successful?

About 190 million individuals and their families across the world are served by more than 3,500 MFIs spanning Latin America, North America, Asia, Africa, Europe and Australia, including countries like the USA, Canada, Great Britain and Norway (Daley-Harris 2009; De Aghion and Morduch 2004; Reed 2013). Thus, MFIs exist not only in countries that are considered part of the developing world but also in many of the rich, developed economies of the world. The flagship example of how successful microfinance can be comes from Bangladesh, where the Grameen Bank currently serves more than seven million clients (De Aghion and Morduch 2004; Reed 2013).

The majority of MFIs are not financially self-sufficient and operate on subsidies provided by governments as well as institutional and private donors (Brau and Woller 2004; Morduch 2000). The importance of achieving sustainability is the subject of a major debate in the microfinance community (reviewed in Brau and Woller 2004; Morduch 2000). Some scholars and practitioners advocate that MFIs must be financially self-sufficient in order to be sustainable. Others emphasise the social returns of microfinance and believe that sustainability can be achieved without self-sufficiency via contributions from committed donors. While the former group are in favour of raising interest rates, arguing that people 'require access to credit, not cheap credit', the latter argue that financial self-sufficiency often involves trading off reaching the poorest borrowers against reaching large numbers of borrowers (reviewed in Brau and Woller 2004; Morduch 2000). The global median interest rate in 2011 was 27 %, but interest rates vary widely ranging from about 15 to greater than 80 % (Rosenberg et al. 2013). Unsurprisingly, for-profit MFIs collect higher average interest yields than non-profit MFIs.

Several authors argue that microfinance programmes have been used by loan-takers more as an income-smoothing instrument, to tide over cash-flow problems, rather than as a source of capital for long-term investments in business initiatives (De Aghion and Morduch 2004; Ito 1998; Rutherford 1999). There is variation in rates of loan repayment and the degree of self-sustainability of MFIs both within and across countries (reviewed in Brau and Woller 2004; De Aghion and Morduch 2004; Morduch 1999). It is so far unclear whether microfinance has produced significant and sustained positive impacts for its potential beneficiaries (Buckley 1997).

3.1.3 The Microcredit Model and How it Links to Evolutionary Theory on Cooperation

Most microcredit programmes are based on the model of 'group lending with joint liability' (Hermes and Lensink 2007). Here, I explain what this means. Typically, when an individual wishes to take a loan from a bank, he or she needs to present the bank with collateral, often land or property, which the bank may keep in the event that the loan-taker is unable to repay the loan. The collateral therefore serves as a guarantee that the loan-taker will repay the loan. Consequently, individuals who are unable to provide collateral, if for instance they do not own any land or property, are unable to take out a loan. In this way, individuals from low-income households are excluded from mainstream banking services. The microcredit model of 'group lending with joint liability' removes the requirement for monetary collateral. It does so by offering loans to groups of individuals who are jointly liable for them. Most often this means that if the group is unable to repay the loan then all group members are barred access to future loans from the programme. For example, if a group of four individuals takes a loan out together and one of them is unable to repay his or her share of the loan, the other three individuals in the loan group are liable to repay this individual's share of the loan if they do not want to be banned from the programme. Hence, in this model of lending, social collateral replaces the traditional monetary one.

The microcredit model of 'group lending with joint liability' creates a cooperative or common-pool resource dilemma. An individual can take out a loan with a group of other individuals and then refuse to pay back his or her share of it, knowing that the other individuals in the loan group would still be liable to pay his/her share. Thus, successful repayment of the loan is contingent upon at least some members of the loan group cooperating to repay it. This can be achieved either if all group members repay their share of the debt (i.e. they all cooperate) or if some members repay the shares of other group members along with their own shares (i.e. some cooperate and others cheat). Since successful repayment of the loan is contingent on individuals solving the cooperative dilemma, factors that encourage and maintain cooperation within loan groups should also improve loan repayment and therefore the success of MFIs. Many MFIs across the world report repayment rates greater than 90 % (Brau and Woller 2004), although most studies do not report the percentage of loans that are repaid equitably by all loan-group members.

Economists are well aware of the cooperative dilemma at the centre of the microcredit model, and a vast and ever-growing literature in economics has been identifying factors that are associated with loan repayment. An equally prolific literature in the evolutionary sciences is devoted to identifying what drives the evolution and maintenance of cooperation in a range of cooperative dilemmas. Thus, if evolutionary theory is effective at explaining human behaviour in the real world and cooperation is central to ensuring loan repayment in microfinance schemes, then we should expect a correspondence between the findings of these two independent bodies of literature. In other words, factors associated with loan repayment should also be those identified by evolutionary theory as important for the maintenance of cooperation. In the remainder of this chapter, I test this hypothesis by presenting and comparing findings from these two independent literatures.

Note that I am not suggesting that the only factors that affect the success of MFIs are factors that encourage cooperation. Indeed, not all microcredit programmes are based on the model of group lending via joint liability (although a survey conducted by Lapenu and Zeller (2001) in Africa, Asia and Latin America found that more than two-thirds of surveyed borrowers are served by group-lending programmes). Moreover, there is substantial variation in the structure of MFIs (Brau and Woller 2004; Hermes and Lensink 2007) which could also influence rates of loan repayment in ways that are unrelated to solving the cooperative dilemma posed by group-lending.

3.2 A Brief Review of the Evolutionary Literature on Cooperation

In this section I briefly review findings from the evolutionary literature on cooperation. Cooperation is defined as a behaviour that is beneficial to the recipient of the act, often (but not necessarily) at a cost to the actor (West, Griffin and Gardner 2007a). From an evolutionary perspective, the puzzle of costly cooperation is as follows: How does costly unselfish behaviour evolve and persist in a population where selfish individuals (defectors) would be more successful in the short term? The problem arises when cooperators repeatedly interact with selfish individuals who in the role of recipients always benefit from cooperators but as actors never bear the cost of cooperation. Such selfish individuals are expected to outcompete cooperators.

A general solution to this puzzle is to ensure that cooperators only ever interact with other cooperators (Fletcher and Doebeli 2009, 2010; Fletcher and Zwick 2006; Queller 1985, 1992). Hence, the evolution of cooperation requires mechanisms that allow cooperators to interact with each other at a higher probability than they do with defectors. Mechanisms that increase the likelihood that a cooperative individual is in a group with other cooperators promote the evolution of cooperation (Fletcher and Doebeli 2009, 2010; Fletcher and Zwick 2006; Queller 1985, 1992). Over the last half-century, many such mechanisms have been proposed (Nowak 2006; Sachs, Mueller, Wilcox and Bull 2004; West, Griffin and Gardner 2007b). Here, I focus on three that I think may be important in the context of microfinance.

3.2.1 Common Ancestry (Kin effects)

Cooperation can evolve when help is preferentially directed towards genetic relatives of the focal individual (Hamilton 1964a, 1964b, 1975). Kin selection (Maynard Smith 1964) describes the specific circumstance where cooperation evolves due to the actor and the recipient sharing ancestry. Common ancestry is a reliable indicator that the recipient of cooperation shares genes, including the cooperation allele[1], with the focal individual (Grafen 2007, 2009) and is therefore also likely to exhibit the cooperative phenotype[2]. Limited dispersal in multigenerational populations or the collective dispersal of relatives in groups promotes the association of relatives and the action of kin selection (Gardner and West 2006; Hamilton 1964a;

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[1] An allele is one of a number of alternative forms of a gene such that each allele has a different effect on the organism. For example, a gene for height may have many alleles specifying different heights.

[2] A phenotype is an observable characteristic or trait of an organism, such as its behaviour, morphology or physiology. Phenotype is not necessarily completely determined by an organism's genes as it can be influenced by other factors such as the environment.

Irwin and Taylor 2001; Kümmerli, Gardner, West and Griffin 2009; Mitteldorf and Wilson 2000; Nowak, Bonhoeffer and May 1994; Nowak and May 1992; Taylor and Irwin 2000; West, Pen and Griffin 2002).

Kin selection is contingent on the availability of information about common ancestry. This information need not be processed consciously and may most commonly be obtained from spatial cues such as a shared nest, colony or household, or phenotype-matching when interacting individuals can estimate genotypic similarity based on phenotypic (trait) resemblance (Hamilton 1964b; Holmes and Sherman 1982; Lacy and Sherman 1983; Lehmann and Perrin 2002; Reeve 1989; Sherman, Reeve, and Pfennig 1997).

There is substantial empirical evidence that humans favour kin across domains such as food sharing (Gurven, Hill and Kaplan 2002; Gurven, Hill, Kaplan, Hurtado and Lyles 2000; Marlowe 2010), cooperative hunting (Alvard 2003; Morgan 1979), providing financial aid (Bowles and Posel 2005), child care (Anderson, Kaplan, Lam and Lancaster 1999; Flinn 1988; Marlowe 1999), mitigation of conflict (Chagnon and Bugos 1979; Daly and Wilson 1988a, 1988b) and even in their willingness to suffer physical pain to benefit someone in an experimental context (Madsen et al. 2007).

3.2.2 Prior Interaction

Cooperation can evolve when help is preferentially directed towards individuals who are known cooperators (Alexander 1987; Aoki 1983; Axelrod 1984; Brown Sanderson and Michod 1982; Trivers 1971). Knowledge of the recipient's prior cooperative history may come from the focal individual's own previous interaction with them (Axelrod and Hamilton 1981; Trivers 1971) or from knowledge of others' prior interactions with them (Leimar and Hammerstein 2001; Lotem and Stone 1999; Milinski, Semmann, and Krambeck 2002a; Mohtashemi and Mui 2003; Nowak and Sigmund 1998a, 1998b; Panchanathan and Boyd 2003, 2004). In this case, an individual's prior behaviour acts as a reliable indicator of the likelihood that he/she will exhibit the cooperative phenotype in the future. Reciprocal cooperation (also known as reciprocal altruism) is called 'direct' (Trivers 1971) if individuals interact repeatedly with the same partner, and 'indirect' (Alexander 1987) if they interact on repeated occasions with a set of partners but only once with any particular member of that set.

The two conditions necessary for reciprocal cooperation to evolve are (1) repeated interactions between the same (direct reciprocity) or different (indirect reciprocity) individuals and (2) information or memory of the outcome of the previous interaction (direct reciprocity) or cooperative reputation of the partner (indirect reciprocity). The availability of information or memory of a partner's prior behaviour is thus essential for reciprocity to evolve. It is unclear whether reciprocal cooperation can lead to stable cooperation in a population if individuals make errors, possess imperfect memory or information and participate in limited interactions (reviewed by Lehmann and Keller 2006). Reciprocal cooperation is also unlikely to evolve when reciprocating groups are large (Boyd and Richerson 1988).

There is strong, accumulating empirical evidence from laboratory experiments and field studies that humans demonstrate both direct reciprocity (Clark and Sefton 2001; Fehr and Gächter 1998; Gächter and Falk 2002; Gurven et al. 2002; Gurven, Hill, et al. 2000; Gurven 2004a, 2004b; Kaplan and Hill 1985; reviewed in Fehr and Fischbacher 2003 and Gächter and Herrmann 2009) as well as indirect reciprocity (Alpizar, Carlsson and Johansson-Stenman 2008; Milinski, Semmann, Bakker and Krambeck 2001; Milinski et al. 2002a; Milinski, Semmann and Krambeck 2002b; Seinen and Schram 2006; Wedekind and Braithwaite 2002; Wedekind and Milinski 2000; reviewed in Fehr and Fischbacher 2003 and Gächter and Herrman 2009). However, studies of food sharing in small-scale societies have reported the high frequency of reciprocity among kin (Allen-Arave, Gurven and Hill 2008; Gurven, Hill, et al. 2000). Kin selection and reciprocity may therefore augment and stabilise each other in establishing cooperation in these populations.

3.2.3 Assortation or Partner Choice

Cooperation can evolve when help is preferentially directed towards individuals specifically sharing the cooperative allele with the focal individual (Grafen 2009; Hamilton 1964a; Lehmann and Keller 2006; Wilson and Dugatkin 1997). Theoretical models vary based on the mechanism by which such assortment is achieved. For instance, linkage disequilibrium between the allele responsible for cooperation and another allele encoding some phenotypic trait (a green beard for example) allows individuals to identify others possessing the cooperation allele (Haig 1997; Jansen and van Baalen 2006). An alternative and earlier formulation of the 'green beard effect' specifies a single complex gene coding for both cooperative behaviour as well as the phenotypic trait indicating its presence in an individual (Dawkins 1976; Hamilton 1964a, 1964b). In other models, individuals assort based only on whether they are similar with reference to an arbitrary characteristic or tag (Axelrod, Hammond and Grafen 2004; Riolo, Cohen and Axelrod 2001). In all these models, individuals' phenotypes for the 'green beard' gene or tags act as reliable indicators of whether they are likely to exhibit the cooperative phenotype. The maintenance of linkage between 'green beard' and cooperative genes is essential for cooperation to evolve via this mechanism. Since mutation and recombination are likely to break down such linkage, 'green beard' effects are generally considered unstable (Blaustein 1983; Dawkins 1976; Lehmann and Keller 2006).

The evidence pertaining to tag-based recognition of cooperators in humans is mixed. While some experimental studies suggest that people can use facial and other cues to identify likely cooperators (Fetchenhauer, Groothuis and Pradel 2009; Pradel, Euler and Fetchenhauer 2009; Verplaetse, Vanneste and Braeckman 2007), there is considerable evidence demonstrating that most humans, including trained policemen, can detect likely cheaters no better than chance (Aamodt and Custer 2006; DePaulo, Stone and Lassiter 1985; DePaulo 1994; Ekman and O'Sullivan 1991; Zuckerman and Driver 1985). It has been suggested that culturally inherited traits like accents, rituals and practices or adornments, as well as arbitrary behavioural signals such as secret handshakes, may serve as tags (Riolo et al. 2001).

Cooperation can also evolve as a costly signal indicating the underlying quality of an individual as a potential mate, friend or ally (Gintis, Smith and Bowles 2001; McAndrew 2002; Roberts 1998; Zahavi 1997). In this case, the cooperative allele itself acts as a tag and a reliable indicator that the focal individual possesses some other fitness-enhancing trait which makes him/her a desirable mate or interaction partner (Miller 2007). There is empirical evidence that in humans cooperative behaviour enhances individuals' status and standing, affording them social advantages in the long run (Alvard and Gillespie 2004; Birkás, Bereczkei and Kerekes 2006; Gurven, Allen-Arave, Hill and Hurtado 2000; Hawkes and Bird 2002; Sosis 2000; and reviewed in Miller 2007).

3.3 A Brief Review of the Economic Literature on Microfinance

In this section, I review findings from the literature on microfinance regarding factors that affect loan repayment performance. I have organized these findings based on the three mechanisms that I outlined in the previous section, considered important for the evolution and maintenance of cooperation. This facilitates comparison between the two bodies of literature. Note that the reviewed studies all analyse the repayment rates of loan groups and not those of their individual members.

3.3.1 Kin Effects

A relatively small number of studies have explicitly examined whether the presence of kin in a loan group facilitates repayment. In a study conducted among 128 loan groups across three group-lending programmes in Bangladesh, Sharma and Zeller (1997) found that repayment problems increase when there are more relatives in the group. Similarly, Ahlin and Townsend (2007) found a significant negative association between the percentage of close relatives in the group and repayment rate among 262 loan groups in Thailand. Both these papers suggest that individuals might find it difficult to impose penalties on relatives in order to ensure loan repayment. In their review, Hermes and Lensink (2007, p. 3) suggest that 'screening, monitoring and enforcement among relatives does not take place or at least is less effective, since relatives may more easily collude against the programme and delay repayment'.

Ahlin and Townsend (2007) examined whether cooperation or sharing between loan group members in other activities was associated with repayment performance. They formulated a sharing index measuring whether individuals had helped loan-group members with money or free labour, coordinated the transport of crops, the purchase of inputs or the selling of crops. The sharing index was also calculated separately for relatives and non-relatives in the group. They find that if they pool relatives and non-relatives together in the analyses, then sharing is negatively associated with repayment. This result is intriguing and may be further evidence that enforcement is difficult when group members have close relationships, indicated here by the degree of sharing between them. However, upon distinguishing between relatives and non-relatives, the authors find that sharing among non-relatives remains negatively associated with repayment whereas sharing specifically among relatives is positively associated with it. Thus, perhaps kin that share with each other reciprocally are less likely to freeride and therefore less likely to require enforcement. Much like Allen-Arave et al. (2008) and Gurven et al. (2000) found in their studies of food sharing, kin effects and reciprocity may augment and stabilise each other in establishing cooperation and effective loan repayment.

In contrast to the above-described studies, Al-Azzam, Hill and Sarangi (2012) found no significant association between the number of relatives in the group and repayment performance across 160 loan groups in Jordan. Since the studies described in this section measured the repayment performance of loan groups and not the individual repayment performance of each group member, their findings suggest that in the case of a deficit, kin do not appear to repay each other's shares any more than non-kin group members do.

3.3.2 Prior Interaction

Several studies have investigated the effects of pre-existing social ties, past interactions and frequency of meetings on rates of loan repayment. These are all factors that are likely to indicate the extent to which individuals have reputational information about their group members, which as described in Sect. 3.2.2 is another mechanism by which cooperation can evolve. Zeller (1998) found that the number of social bonds between group members, such as whether they belonged to the same village, hamlet, ethnicity, extended family and religion, has a significant positive association with repayment rates in 146 loan groups across six lending programmes in Madagascar. In contrast, Wydick (1999) showed in a study conducted in Guatemala that social ties within groups, measured as the number of years individuals were acquainted before they formed the group, whether all members were friends and whether they were involved in any joint social activities, appeared to have no significant effect on repayment; if anything, the direction of the association was negative for all three variables. Similarly, Ahlin and Townsend (2007) found no association between repayment and the percentage of group members living in the same village in Thailand.

The loan groups included in most of the above studies were formed non-randomly, i.e. members chose their group members. This creates a problem of 'endogeneity' or autocorrelation so that it is difficult to disentangle the causal effects of social ties from any other variables that influenced group formation. Dean Karlan's (2007) study avoided this problem by studying 2,000 individuals in Peru who were randomly designated by the MFI to different loan groups; this allowed him to disentangle the effects of social connections from other variables that affect group formation. He found that individuals who live in closer geographic proximity to their group members are more likely to repay loans and save more. He suggests that this is because group members are better able to monitor each other and enforce repayment. He empirically demonstrated that individuals who knew each other before joining the loan group had more accurate information about each other's prior default histories; this suggests that the reason that social connections may improve loan repayment is that they increase the availability of reputational information. Karlan (2007) also shows that members can distinguish between strategic defaults and defaults due to external shocks and bias punishment towards the former type of default. Wenner (1995) found that loan groups in Costa Rica that screened members on the basis of their reputations showed better repayment performance than those that did not.

In a study using economic games mirroring a microfinance scheme, Cassar, Crowley and Wydick (2007) find that simple acquaintanceship is not adequate to improve repayment performance; this study was conducted in South Africa and Armenia. Instead, those who have been helped by others in the past (when faced with exogenous shocks) are more likely to contribute in a subsequent round of the game. Note that this study was conducted with an all-female sample.

Feigenberg, Field and Pande (2013) performed an experimental intervention with an MFI in India, where they randomly varied the frequency with which groups met (weekly vs. monthly) during the first loan cycle. The results show that more frequent meetings are associated with increases in long-term social interaction and lower default rates. In contrast, van Bastelaer and Leathers (2006) found that the frequency of group meetings was negatively associated with repayment rates in rural Zambia. However, the farmer loan groups included in this study decided themselves how frequently they met. Thus, these authors suggest that in this case, the negative relationship between frequency of meetings and repayment rates may result from reversed causality where groups with widespread non-repayment hold more frequent meetings in order to improve repayment. Interestingly, Abbink, Irlenbusch and Renner (2006) found that repayment rates decreased as individuals approached the end of a microfinance game experiment as one might expect if individuals realized that future opportunities for reciprocity would be low.

3.3.3 Assortation or Partner Choice

Most MFIs encourage loan groups to form endogenously, i.e. individuals select their group members themselves. Theoretical work on microfinance predicts that this self-selection process used in most group-lending schemes should improve repayment rates by mitigating adverse selection[3] in credit markets and thus lowering

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[3] When lenders cannot differentiate risky borrowers from safer ones, they cannot differentially charge riskier clients higher interest rates. This raises the average interest rate for all clients and therefore drives safer clients out of the credit market and increases the proportion of risky clients that the lender now caters to. This is known as adverse selection.

the cost of borrowing (Ghatak 1999; Van Tassel 1999). However, few studies appear to have investigated whether self-selecting groups perform better than groups that have been allocated randomly by an MFI, perhaps since most MFIs use the same mechanism of group formation and do not vary much in this respect. Among these is a study by Sharma and Zeller (1997), which found that groups formed via self-selection of group members did show better repayment performance. In contrast, Wydick's (1999) study of Guatemalan MFIs finds no difference between the repayment rates of groups comprising acquaintances compared with those consisting of strangers.

A number of authors have investigated the effects of assortation on loan repayment by using economic game experiments played both in a laboratory with student subjects and under field conditions with individuals who are most likely to use microfinance. Abbink et al. (2006) conducted a laboratory experiment using a microfinance game with student subjects and found that while self-selected groups contributed more in the first round, cooperation declined among these groups in later rounds. On the other hand, they found that while repayment in randomly chosen groups started lower, it declined more slowly as rounds progressed than it did in the self-selected groups. Giné, Jakiela, Karlan and Morduch (2010) demonstrated that allowing groups to self-select members increased repayment rates in a microfinance game played with small enterprise owners and employees in Lima.

Another way to examine the effects of assortation on loan repayment is to test whether groups that are socially and culturally more homogeneous have better repayment performance. Karlan (2007) found that cultural homogeneity was associated with better repayment performance in Peru. Similarly, Cassar et al. (2007) found that social and cultural homogeneity improves loan repayment in a laboratory microfinance experiment conducted in South Africa and Armenia. In contrast, Paxton, Graham Douglas and Thraen (2000) found a negative association between group homogeneity and repayment in Burkina Fasso, and Kritikos and Vigenina (2005) found no association between the two in Georgia. Similarity in age or levels of education had no significant impact on repayment in a study conducted in Bangladesh (Godquin 2004).

Hence, there is mixed evidence that assortation improves loan repayment in microfinance schemes. These findings need to be interpreted carefully because, as mentioned previously, few studies may have been able to test for the effects of assortation since MFIs do not vary much for this variable; the studies that have done so produced mixed findings. Studies using controlled experiments, on the other hand, all produce similar findings that suggest that self-selection enhances repayment performance.

3.3.4 Laboratory Experiments

Recent research has begun to use laboratory experiments to investigate behaviour in the context of microfinance schemes. A particularly interesting study by Dean Karlan, conducted among 41 female borrowers in Peru, investigated how well behaviour in laboratory experiments reflects the behaviour of individuals participating in microfinance schemes. Karlan (2005) found that more ‘trusting’ first-players in a trust game were more likely to have repayment problems when examining microfinance data collected 1 year after the experiment. On the other hand, ‘trustworthier’ second-players in the trust game displayed higher likelihoods of loan repayment. However, he found no relationship between repayment performance and behaviour in a public goods game.

Cassar et al. (2007) played a microfinance game with 498 individuals across 36 groups in South Africa and Armenia. They found that individuals’ ‘trusting’ behaviour in a trust game is not associated with loan repayment in a microfinance game. However, similar to Karlan (2005), they found that ‘trustworthiness’ in the trust game was positively associated with loan repayment in the microfinance game.

3.4 Conclusion

The studies reviewed in Sect. 3.3 demonstrate that there is mixed evidence in the economic literature that the three evolutionary mechanisms considered here (kin effects, reciprocity and assortation) affect loan repayment in the predicted direction. While some studies on MFIs support the findings of the evolutionary literature on cooperation, others do not.

There are several potential explanations for these mixed results. One possibility is that the cooperative dilemma inherent to the microcredit model of group lending via joint liability does not affect loan repayment and as a consequence (or otherwise) evolutionary theory on cooperation does not apply to microfinance. While this hypothesis cannot be rejected at this stage, I think that it is unlikely to explain my findings. This is because I find that there is mixed support for evolutionary models in the microfinance literature as opposed to no support. Indeed, some studies do find evidence in favour of the evolutionary theories that I have considered in this chapter. Moreover, successful repayment of the loan necessarily involves cooperation either from all individuals in the loan group or from some individuals who pay not only their share but also the shares of defaulting members. The overall repayment rates of many MFIs are very high. For instance, Grameen Bank in Bangladesh has reported repayment rates greater than 95 % for most of its life (De Aghion and Morduch 2004; Morduch 1999). These data suggest that at least some members of loan groups are cooperating to repay these loans.

The studies reviewed here were conducted in different parts of the world with people living in different environments and not all mechanisms were considered and compared in each study. Since natural selection operates in the context of a particular environment, different mechanisms might operate to produce cooperation in these different environments, leading to mixed support for any one mechanism. Furthermore, there may be a trade-off between factors that allow individuals to screen good partners for cooperation and those that allow them to enforce it within a group once it has formed; this could lead to mixed findings. For example, an individual may be most likely to cooperate with kin but least likely to punish them. In this case, individuals may choose to be in loan groups with kin but if enforcement is important for ensuring loan repayment, they may be unable to ensure cooperation and therefore loan repayment.

In this chapter I focussed on three major mechanisms that can support the evolution of cooperation. Recent theory and empirical research on the evolution of large-scale cooperation argue that culturally transmitted norms may be an important driver of variation in levels of cooperation across human populations (Boyd, Gintis, Bowles and Richerson 2003; Boyd and Richerson 1985; Choi and Bowles 2007; Gintis 2003; Guzmán, Rodríguez-Sickert and Rowthorn 2007; Henrich et al. 2012; Henrich 2004; Henrich et al. 2005, 2006, 2010). Other studies highlight the crucial role that demographic and ecological factors play in shaping cooperative behaviour (Lamba and Mace 2011, 2012, 2013). Indeed, there is some evidence that factors like sex (D'Espallier, Guérin and Mersland 2011) and loan-group size (van Bastelaer and Leathers 2006; Zeller 1998) are associated with loan repayment. Hence, cultural norms and/or demography may also play an important role in determining the success of MFIs.

At the beginning of this chapter I described my motivation for undertaking this study. I think that the above analyses demonstrate the utility of evolutionary theory as a hypothesis-generating tool that systematises the study of human behaviour. Although I present only a preliminary, qualitative and coarse-grained comparison of two vast bodies of literature, both very technical, my mixed findings raise many questions that warrant further deliberation and may inform researchers in both disciplines.

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Chapter 4
How Development Intervention Drives Population Change in Rural Africa: A Case Study of Applied Evolutionary Anthropology

Mhairi A. Gibson

Abstract Rural development initiatives across the developing world are designed to improve community well-being and livelihoods; however, they may also have unforeseen and sometimes negative consequences. This chapter reviews evidence from a series of studies grounded in the framework of evolutionary life history theory demonstrating that the introduction of a recent rural development project has been the catalyst for population changes in rural Ethiopia. Specifically, it identifies that a rural intervention scheme, which aimed to enhance maternal health and child survival through improved water supplies, has also underpinned increases in family sizes introducing greater scarcity of resources within the household. This in turn is linked to an increased outmigration of young adults to urban centres over a 15-year period. In the context of declining ratio of agricultural land to people and few off-farm jobs, this outmigration for employment or education is likely to represent a strategy of resource diversification for intensely competing offspring. I discuss the wider implications of this body of work for improved understanding of the processes which initiate rural-to-urban migration, transitions to low fertility as well as the design and implementation of development intervention across the less developed world.

4.1 Introduction: Population and the Impact of Development

Projections that the world population will peak at 9 billion, then start to slowly decrease before the end of the twenty-first century, have led to a recent focus on problems raised by replacement fertility and population implosion (Lutz and Sanderson

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2004). The inference is that population growth is a feature soon to be relegated to human history. However, for many of the poorest countries, population growth is expected to continue into the next century (United Nations 2011). In these contexts, population expansion is hampering economic growth and the financial security of nations and individuals (Bloom and Canning 2008). The implications are numerous (Bongaarts and Sinding 2011). High fertility leads to a young population which competes for often scarce and low-paying jobs, and contributes to political instability (Cincotta et al. 2003). Rapid population growth also implies increased demand for already stretched public health services, housing and new employment opportunities in both rural and urban centres. It also raises concerns about environmental degradation and climate change. Recent rises in food and energy prices and the effects of climate change signal pressures on the environment from growing human populations and consumption (Brown 2011).

Development intervention initiatives, many funded by overseas aid, are designed specifically to respond to the needs of these growing populations, often based around the introduction of schemes and technologies which aim to improve livelihoods and well-being. Remarkably, despite the millions of dollars spent on development each year, there is relatively little known about the long-term impact of these projects on the poor (Banerjee and Duflo 2012), particularly the potential for these to introduce unplanned population changes. While many initiatives target and describe immediate benefits linked with improved health and survival, few seek to evaluate unintended behavioural outcomes, e.g. in fertility and migration. Detailed evaluations may not be carried out not only because they are deemed to be expensive, time-consuming and technically complex, but also because they can be politically sensitive, particularly if they are negative (Baker 2000), or suggest the need for further financial investment (Székely 2013). However, successful evaluation of the long-term impact and effectiveness of this aid is of critical importance, particularly in developing countries such as Ethiopia where resources are scarce. If projects are poorly designed or do not reach their intended beneficiaries, they may fail to address or, worse, exacerbate the existing problems.

Evidence-based policy initiatives, shaped by impact assessment trials, are increasingly viewed by both governments and policymakers as providing the most cost-effective solutions to a range of emerging public health, development and social issues (see examples of programmes in Haynes et al. 2012; Banerjee and Duflo 2012). However, few development programmes are grounded in robust theory. Aid agencies have tended to focus on practical rather than theoretical issues, for example addressing immediate needs for a clean water supply or improved health care (Crewe and Axelby 2013). A lack of theory (or one too narrowly defined) may lead to failures in the critical evaluation and monitoring of the costs and benefits of development.

Ethiopia is a good test bed to explore the direct impact of development because significant aid and intervention has only been prevalent since the 1990s, providing researchers with an opportunity to study the changes brought about by development over real time. Today, the country retains a high degree of dependency on international development aid (Alemu 2009): The magnitude of aid has doubled over the past 20 years to $ 1,683 million per annum. Half of the funds used for basic public services, including schools, roads and health care are currently provided by overseas development (World Bank 2009). In spite of increased support, there are questions about the quality and effectiveness of this aid, which is becoming an issue for development practitioners as well as politicians at the local and global levels (Sachs 2005; Moyo 2010). While various development policy and strategy papers address how to manage aid in Ethiopia, few studies exist that document in detail both the direct impact and long-term sustainability of development intervention on local communities.

The aim of this chapter is to explore the troubling paradox that development itself may be one factor driving population change in the poorest countries, producing unforeseen, and in some instances negative, outcomes. I review evidence for the interrelationships between population growth and development in one particular rural Ethiopian community, which has benefited from the introduction of a water development scheme. Combining evolutionary theory with detailed longitudinal demographic and anthropological data and analyses, this research has investigated whether the introduction of village-level tap stands—which reduced women's water-carrying workloads—has contributied to changes in human reproductive biology, parenting behaviour and livelihood strategies. Specifically, it tests an evolutionary life history prediction that reductions in women's energy expenditure will drive higher rates of female fertility, which together with improved child survival will increase family sizes (Gibson and Mace 2006; Kramer and McMillan 2006). Further consequences of population changes are explored, including whether development has increased intrahousehold shortages (Gibson and Mace 2006), educational investment (Gibson and Lawson 2011) and outmigration (Gibson and Gurmu 2012).

This work has been undertaken over a 15-year period in collaboration with a large number of researchers from Ethiopia (including Gurmu, Abate and Tessema) and Europe (Mace, Lawson, Clech and Alvergne). While anthropologists have long worked to ensure the cultural appropriateness of externally generated development plans and technologies (Crewe and Axelby 2013), this case study provides an example of how evolutionary anthropology can guide research and lead to important new insights on the direct impact and effectiveness of development. The following sections include an outline of evolutionary life history theory and its novel predictions, an introduction to the study site and research framework, followed by the main findings and a discussion of the significance of these for development policy.

4.1.1 Evolutionary Life History Theory Predictions

Life history theory is a branch of evolutionary biology which deals with the timing of and allocation of energy towards key components of an organism's life course: in growth and body condition, survival and reproduction. Trade-offs between these key functions have a central role in life history theory (Stearns 1992), based on the assumption that any energy allocated to one component (e.g. growth) must decrease the energy allocated to another (e.g. reproduction). The most-studied human life history trade-offs include those between reproduction and survival; current reproduction and future reproduction; reproduction and growth; reproduction and condition; and number and quality of offspring (for reviews on human life history, see Mace 2000; Lummaa 2007; Lawson 2011). These are predicted to be resolved in favour of reproductive success (numbers of reproducing offspring); however, the best life history strategy is assumed to vary according to local ecological circumstances, e.g. individual condition and local resource availability.

One of the most dramatic human life history trade-offs is that observed between maternal energetic status and reproduction. Studies on human reproductive ecology have revealed that human fertility is responsive to even small changes in maternal bodily condition, identifying both physiological and hormonal pathways along which energetic factors influence reproductive function (Ellison 2001). Reductions in women's nutritional intake, increases in disease prevalence and workloads, which negatively impact on women's energy balance, are all associated with lower female fecundity (Ellison 2003; Ellison et al. 1989) and shortening periods of postpartum amenorrhoea following a birth (Gibson and Mace 2002). These studies also reveal that effects are reversible, so any improvements in women's energy levels may have a positive effect on female fertility. This plasticity in reproductive function (though itself not without limits) is considered to be an evolved response to changing environmental conditions, a mechanism for temporarily delaying energetically expensive pregnancy and lactation during periods of acute resource shortage (Vitzthum 2008; Ellison 1990).

These bio-behavioural responses also raise several novel predictions regarding the impact of water development initiatives, which dramatically reduce women's workload and improve community health. Firstly, that in the absence of contraception and/or clear incentive for fertility limitation, the energy women save may be diverted into reproductive effort and therefore increase female fertility, assuming all else remains equal and that, for example, increased energy is not reallocated to other heavy workload tasks (Kramer and McMillan 2006). Reduced female workloads may also lead to reductions in intrauterine mortality predicting further increases in birth rates. Secondly, the resolution of trade-offs may come at a cost to individual health and well-being over the short term. To maternal health, higher birth rates and a pattern of shorter birth spacing may result in depletion in body condition (Tracer 1991; Sear 2011). Finally, child health and survival may also be compromised, through trade-offs between the quantity and 'quality' of offspring (Lawson et al. 2012; Walker et al. 2008). Larger family sizes brought about by higher birth rates and improved child survival may also trigger household resource shortages, altering parental investment decisions (Gibson and Lawson 2011).

4.1.2 Study Site

This study is based on a rural agropastoralist community of Arsi Oromo, living in a low-lying area of Oromiya region, southern Ethiopia (see map in Fig. 4.1), which suffers from acute, regular water shortages and chronic food insecurity as well as

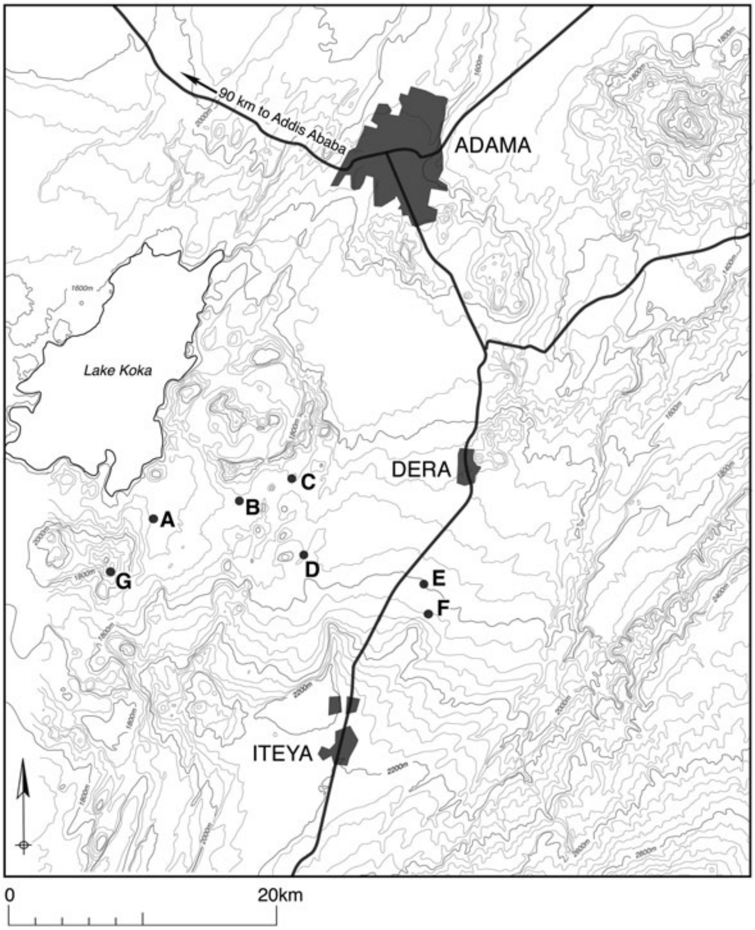


Fig. 4.1 Map of the study site in Arsi Zone, Oromiya, Southern Ethiopia

recent population growth. The Arsi Oromo are representative of many other rural farming communities in Ethiopia, being heavily dependent on agriculture for food supply and income (predominantly cultivating maize, wheat and sorghum). Once described as the 'bread-basket of Ethiopia', in the past two decades the region has experienced poor agricultural productivity arising from the combined effects of environmental degradation and increasingly unreliable rainfall (data from Kulumsa Agricultural Research Station). The villages have limited infrastructure (no electricity or permanent roads) and a shortage of basic public services (markets, schools or adequate health services). Few off-farm employment or income-generation opportunities exist. In 2009, less than 10 % of households had any earnings from non-agricultural activities (Gibson and Gurmu 2012) and many adults remained unschooled and illiterate (35 % of males and 75 % of females were uneducated; Gibson and Lawson 2011).

Use of family planning is limited, though recent evidence suggests that the demand for this is increasing. In 2003, fewer than 3 % of women had ever-used contraception, but by 2009 this figure had increased to 19 % (Alvergne et al. 2011), closer to the national average (Central Statistical Agency [Ethiopia], & ICF International 2012). Obtaining continued and effective supply of modern technologies (predominantly hormonal injections or patches) is problematic. Though there is a planned programme to improve provision in local government clinics, many Arsi Oromo women report using contraception only once as they struggle to find the time or money to repeatedly travel distances to stocked clinics or pharmacies in towns or cities. Family sizes are large: In 2003, the average woman had seven births during her lifetime, a fifth of these children dying within the first 5 years of life.

Increases in agricultural land scarcity, together with few local non-agricultural economic opportunities, have led to a rise in the number of adults migrating to urban centres (rising from < 5 to 20 % over the past 50 years), further facilitated by recent infrastructural improvements in transport and communication links (since 2003). This has included several improved all-season roads, mobile phone reception as well as relaxation of land policies which previously restricted farmers' movement patterns.

4.1.3 The Introduction of a New Labour-Saving Water Supply Scheme

Limited access to clean drinking water has been a major problem in this region (Gibson 2002). Villages are located very far from natural and permanent water supplies, partly due to forced settlement of this population in the mid-twentieth century. Water shortages during the dry season months (December–April) can be particularly severe. Up until recently, a significant amount of time and effort was spent on daily water collection by Arsi women, who bear the brunt of water collection by transporting water on their backs in clay pots (or plastic containers). In some instances, women walking for up to 6 h a day over distances of up to 30 km (Fig. 4.2).

In response to this need, between 1996 and 2000, some villages in the region gained access to a new water development initiative (funded by a UK NGO). The primary goal of this project was to install village-level tap stands, thus improving access to a safe water supply and reducing the time and energy women spent on carrying water (Fig. 4.2). The scheme used gravity to propel the highland spring water through a network of pipelines to community tap stands in low-lying areas (Silkin 1998). Notably, no other community-based activities that might alter health care, family planning, education, income-generating or subsistence-related activities were included.

This development intervention had dramatic effects on women's lives. Following the installation of taps, women's water-carrying loads reduced from on an aver-

Fig. 4.2 Arsi Oromo women collecting water in clay pots (*insera*)

age 3 h per day to 15 min during the driest months (Gibson 2002). Time budget data recording women's weekly activity patterns in 2003 indicated that the time saved in women's water collection was employed in more social activities as well as standing in line at the water tap stand (Abate 2004). The scheme did not alter the water source (highland spring) and quality. However, the quantity of domestic water use increased, despite a small charge levied to each household to cover the cost of a water attendant's salary (employed to ensure that water was not used for feeding livestock or irrigation) (Gibson 2002).

4.1.4 Research Framework

The design and implementation of this particular initiative made it an ideal site for exploring the impact of development. As in many other development projects, limited funds meant that not all villages in the local area were included in the water development scheme, some falling outside an arbitrary administrative boundary that determined in which villages the NGO could operate (local NGO worker, personal communication). This provided a natural experiment where villages with and without access to new water taps could be compared in cross-sectional analyses. Furthermore, since the scheme was recent, it was possible to quantify individual and population changes within villages, before and after the taps had been installed. Longitudinal analyses were used to identify the direct and immediate effects of the arrival of taps on the local population. A summary of the types of analyses undertaken can be found in Table 4.2.

To ensure comparability between the villages included in the study, each was randomly selected from groups which had been matched in relation to a range of parameters (population size, altitude, ethnicity, wealth and distance from the all-weather main road and markets) with the assistance of local NGO workers who had been responsible for tap installation. Since local demand for water was not a factor influencing where the NGOs operated (NGO worker, personal communication), access to improved water supply represented the main difference between villages in the local area (for village characteristics, see Table 4.1).

4.2 Methods and Analyses

4.2.1 Data Collection

Since 2000, collection of demographic, socio-economic and anthropological data has been undertaken in seven villages, including those with and without access to the water development scheme (see Table 4.1). The study population included 7,184 births and 7,038 residents from 1,184 households in 2009, making this one of the largest longitudinal demographic surveys in the country (larger than the Demographic and Health Service for the entire region of Oromiya; Central Statistical Agency [Ethiopia], & ICF International 2012).

During each field season (1999, 2003, 2009), longitudinal and cross-sectional data were collated from all residents across the villages during house-to-house surveys. A broad demographic census and household survey were completed in each, providing data on major socio-economic and demographic factors that may influence population change (e.g. household wealth, household size, individual labour earnings, education and religion). In 2000 and 2003, all ever-married females were interviewed providing full retrospective birth histories, use of contraception and information on water-carrying activities. Child anthropometric data and women's time budget were collected in 2003–2004. In 2009, all household heads were interviewed providing full retrospective migration histories for all household members, including non-resident individuals who had migrated out temporarily or permanently. Migration did not include females who moved between local villages for marriage, common in this patrilocal society.

Table 4.1 Village characteristics

	Village A	Village B	Village C	Village D	Village E	Village F	Village G
Survey	1999, 2003, 2009	1999, 2003, 2009	2003, 2009	1999, 2003, 2009	1999, 2003, 2009	1999, 2003,	1999, 2003
Altitude	1800m	1880m	1880m	1800m	2000m	2000m	1980m
Date taps installed	2000	None	None	1996	1996	1996	2000
Religion	100% muslim	60% muslim, 40% christian	100% muslim	100% muslim	50% muslim, 50% christian	100% christian	100% muslim
Main crop cultivated	Maize	Maize	Maize	Maize	Wheat and barley	Wheat and barley	Wheat and barley
Resident population size (in 2009)	1637	1297	1337	1648	1119	1111*	1006*
No of households (in 2009)	267	240	202	283	192	217*	204*

*In 2000.

Longitudinal data were collected using a detailed events calendar which recorded the timing of all demographic events over the 7–15 years preceding the interview, including the periods before and after the dates of water tap installation (1996 and 2000). Each life history event was dated to the year and to the month or season. A 3-month time period was used for migration histories which covered a 15-year observation window, while a 1-month time period was used to record births and child deaths covering a 7-year observation window. In each case, the calendar was marked with local significant events to assisted memory recall.

To understand local perceptions on recent population changes as well as determine shifts in attitudes, focus group discussions were undertaken with groups of men and women (Fig. 4.3). This included ascertaining views on development, family planning as well as child rearing, education, employment and migration. Quotes from these focus discussions are included in the discussion of the main quantitative findings below.

4.2.2 Analyses

Since the exact timing of the installation of water taps was known (1996 and 2000), a test of the direct impact of development and family dynamics on the probability of birth, death and migration over time was possible using event history (or so-called

Table 4.2 Summary of analyses and main findings

Effect	Type of analyses	Influence of tap installation	Publication
Fertility	Hazards regression, longitudinal analysis of the effect of tap installation on timing of birth	Increased birth rates:	
		Shorter first birth intervals	Gibson & Mace, 2002a
		Reduced post partum amenorrhoea	Gibson & Mace, 2002b
		Shorter inter-birth intervals	Gibson & Mace, 2006
Child Mortality	Hazards regression, longitudinal analysis of the effect of tap installation on timing of child death	Reduced death rates	Gibson & Mace, 2006
Child Growth	Cross sectional analyses comparing tap with non-tap villages	Poorer child growth (height and weight)	Gibson & Mace, 2006
Maternal Condition	Cross sectional analyses comparing tap with non-tap villages	Parity specific decline in body condition (maternal depletion in BMI and MUAC)	Gibson & Mace, 2002b
Child Education	Cross sectional analyses comparing tap with non-tap villages	More children attending school, but greater inequality within households. First born are prioritised over later children.	Gibson & Lawson, 2011
Out-migration	Hazards regression, longitudinal analysis on effect of tap installation on timing of out-migration	Increased out-migration of young adults (15-30y)	Gibson & Gurmu, 2012

hazard) regression analysis. This is a powerful statistical tool for isolating the precise timing of demographic events, e.g. the date of access to taps on the monthly relative probability of child death. Unlike standard forms of regression analysis, it can deal with both censored and time-series data (variables which change through time; Yamaguchi 1991; Allison 1984). Hazards regression modelling analyses were used to explore demographic phenomena in relation to a range of time-varying

Fig. 4.3 Dr Eshetu Gurmu (Addis Ababa University) undertaking focus group discussions in Ethiopian villages

factors for each individual, addressing the impact of (1) the arrival of the new development technology, (2) the arrival of a new birth in the household, (3) the arrival of a spouse, (4) the death or departure of a child and (5) the departure of an adult from the household. Additional cross-sectional analyses were permitted by comparing the tap villages with comparable neighbour villages which had never benefited from new water tap stands.

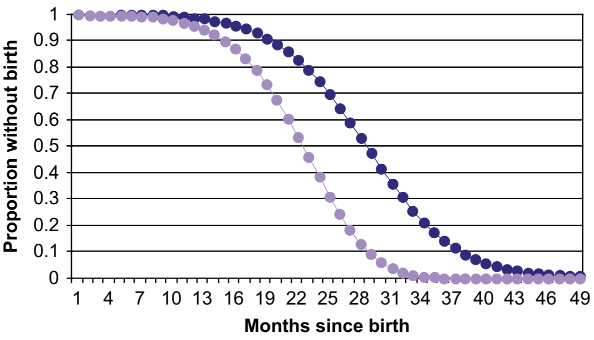
Analyses were undertaken using multivariate models to assess the partial effects of a range of socio-demographic and economic factors known to influence the dependent variables, including village, age, sex, household wealth, education levels, family size and birth order. Longitudinal data were analysed using hazards regression modelling, whereas cross-sectional data were analysed using generalised linear model (GLM) and logistic regression. To control for family effects (i.e. to explore variation between families), multilevel modelling techniques were employed in some analyses, with household identity set as a random effect.

4.3 Results

4.3.1 Fertility

Improved access to water was associated with increased monthly probability of child birth, indicating shorter inter-birth intervals. The odds of a woman with access to taps giving birth in any given month were three times greater than a woman without access to an improved water supply (Gibson and Mace 2006). Significant interaction terms between water tap access and time indicated that the effect of taps on the risk of birth varied over months since birth: Water points had the greatest influence on fertility during women's most fertile period 18–36 months postpartum (Fig. 4.4). There were a number of other significant and expected socio-

Fig. 4.4 Kaplan–Meier/survival plot of timing of next birth (inter-birth interval; with taps: *light font*, without taps: *dark font*)



demographic predictors of women's birth rates, e.g. the death of a previous child which had a positive influence on women's monthly risk of birth (Gibson and Mace 2006), due to premature cessation of breastfeeding and associated amenorrhoeic effects (Gibson and Mace 2002b). Younger maternal age and lower parity were all significantly associated with higher birth rates (Gibson and Mace 2006). In support of the notion that water-carrying workloads may influence female fertility, women's water-carrying method was also a significant predictor of birth rates (after controlling for wealth and other socio-demographic factors). On average, women who exclusively carried water on their back had birth rates 50% lower than those who had lesser loads, due to use of donkey or assistance from kin (Gibson and Mace 2002b). Furthermore, focus group discussion revealed that local people viewed the introduction of new tap stands as influencing fertility, in the words of a female informant, *'Women give birth all day and night…women are taadhi [fertile], and space between children is shorter. The time between the marriage and the first child is less than 1 year, previously it was around 3 years'.*

We have argued that the observed increase in birth rates linked with the introduction of taps is mediated by improvements in women's workloads (Gibson and Mace 2006). This has been brought about by reducing energy expenditure on water collection rather than changes in health, breastfeeding practices, food intake or coital frequencies. A cross-sectional health survey in 2003, in which women reported any ill health they had experienced during the two preceding weeks and any health-seeking behaviour, indicated that improved water supply had not improved women's health (one-third of women reported ill health and had attended a health clinic in both tap and non-tap villages; Gibson and Mace 2006). Neither had it altered breastfeeding practices. Women with access to taps did not use their surplus energy to breastfeed for longer periods of time—time to full weaning was on an average 37 months for women with and without access to taps (Gibson and Mace 2002b)—though the frequency or intensity of breastfeeding, which was not measured, may have increased among these women.

Anthropometric data revealed that women's nutritional status (body mass index, BMI or sum of skinfolds) remained unchanged in tap villages. For example, BMI averaged out at 20.48±2.02 in villages without taps and 20.06±2.02 in villages with taps (Gibson and Mace 2002b). This finding indicated that despite reducing workloads, development had not increased women's energy balance to the extent that they gained additional weight. However, shifts in female fecundity are still possible. A study conducted in rural Poland has revealed that reproductive hormones may be sensitive to any change in workload, even prior to changes in energy balance represented by weight loss or gain (Jasienska and Ellison 1998). In addition, the observed reductions in water-carrying workload may have reduced foetal loss in pregnancy.

Finally, a reduction in workload may have resulted in increased opportunities for sex; however, we argue that higher coital frequencies are unlikely given that men's workloads have not been affected by the labour-saving technology (and women have little autonomy within the household). On balance, these findings lend support to the life history theory predictions that surplus energy from the labour-saving technology had been diverted directly towards reproduction, through improved ovarian function and/or reduced intrauterine mortality.

4.3.2 Mortality

Improved access to water was associated with a reduced probability of child death. The monthly relative risk of child death was 50 % lower for individuals gaining access to the new water tap stand (Gibson and Mace 2006). The accelerated probability of child survival with the new water supply was most apparent in the first year of life. However, the absolute benefit of water availability was retained up to 3 years of age (Fig. 4.5). Local government health surveys suggest that the observed reductions in mortality have been due to a drop in waterborne diseases associated with poor water supply, particularly diarrhoea and gastroenteritis caused by parasitic, bacterial and viral infections (Gibson 2002; Amudee clinic nurse, personal communication). This is supported by evidence from focus group discussions which revealed that the arrival of taps is widely perceived to have improved hygiene and water consumption as well as reducing women's workloads. In the words of a local informant, *'There are many changes since the water development. The task of collecting water is easier for women. We are no longer rationing water for our children. We can wash ourselves more frequently'.*

4.3.3 Nutritional Status

Malnutrition and poor child growth were prevalent in the villages, due to years of food shortages following crop failure. In an anthropometric survey in the study villages in 2003 (7 years after the taps were first installed), a third of all children under 15 years of age were seriously malnourished ($n = 654$; weight-for-age Z-score (WAZ) < -2), half were seriously stunted (height-for-age Z-score (HAZ) < -2) and 20 % of women had a BMI of below the 18.5 cut-off used to define chronic energy

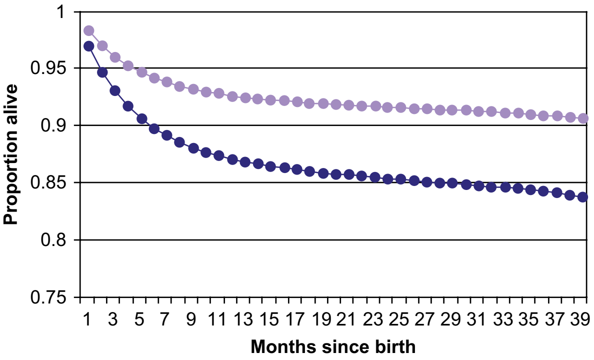


Fig. 4.5 Kaplan–Meier/survival plot of timing of mortality events (with taps: *light font*, without taps: *dark font*)

malnutrition (Gibson and Mace 2006). However, these data also provided some indication that larger surviving family sizes have had an additional negative impact on child growth and maternal body condition in tap villages.

Children living in tap villages had worse nutritional status than those living in non-tap villages. After controlling for the effects of age, sex, birth order, socio-economic status and family size, children living with access to taps were at a significantly greater risk of being malnourished (low WAZ; GLM beta coefficient $=-0.278\pm0.11$, $t=-2.50$, $p=0.013$) and stunted (low HAZ; GLM beta coefficient $=-0.303\pm0.15$, $t=-1.98$, $p=0.048$; Gibson and Mace 2006). This effect was particularly noticeable for children under the age of 5, indicating that only those born since the installation of taps (since 1996) had lower nutritional status. There are two possible explanations for the observed increase in levels of malnutrition relating to improved survival and increase in family size. Firstly, there is greater competition between siblings for limited household resources, particularly food (a quality–quantity trade-off; Weaver and Beckerleg 1993). Secondly, there has been a sample selection effect (due to improved survival of low-birthweight babies). The latter is perhaps the most likely explanation. If siblings were competing with one another for food then poor growth should have been recorded across children of all ages; instead, higher levels of malnutrition were found only among children born since taps were installed. We have argued that due to enhancements in maternal energy budgets brought about by labour-saving technology, smaller lower-birthweight offspring were surviving critical periods of prenatal life and early childhood and thus being recorded in our survey (Gibson and Mace 2006). Other studies examining the impact of health interventions in natural fertility populations have failed to find dramatic improvements in child growth patterns, possibly for similar reasons. For example, attempts to reduce diarrhoea prevalence among children did not improve child growth levels in either rural Gambia or Bangladesh (Briend et al. 1989; Poskitt et al. 1999).

Despite reductions in women's workloads, there is evidence that high birth rates and shorter birth intervals have also had a negative effect on women's body condition (BMI, as a proxy measure for % body fat). Women with high parity (six or more offspring) had lower BMI than similar-aged counterparts with two fewer births (dropping from an average 20.6 to 19.7 BMI; Gibson and Mace 2002b). In addition, women with short inter-birth intervals were in worse body condition. These effects were found across all villages, most likely due a combination of high fertility and low nutrition which resulted in particularly severe energetic stress on women (Gibson and Mace 2002b; Tracer 1991; Sear 2011). Shorter birth spacing and poor maternal condition were perceived locally as having a significant negative impact on child health, *'...problems [of ill health] begin in the mother's stomach. Mothers are weaker now'* (Male village informant).

4.3.4 Child Education

One of the benefits of development intervention has been an increased uptake of existing educational opportunities among the Arsi Oromo. In 2003, over a third of children (37.1 %) with access to improved water supply attended the local school (which was of equal distance from each village), while ~10 % fewer did so from non-tap neighbouring villages (Gibson and Lawson 2011). These findings suggest that parenting attitudes and investment behaviours have changed with the development intervention. One possible explanation for the shift is that, following the reduction of extrinsic child mortality risks (those beyond parents' control) associated with poor water supply, parents may perceive that they have a greater influence on the success of their children more generally (Gibson and Lawson 2011). Educating children is a costly activity for parents, both in terms of opportunity costs with time spent away from productive agricultural activities and also in terms of material resources (e.g. money for books and accommodation). However, with the risk of child death reduced, investment in education may be perceived as more likely to pay off in the long term in terms of jobs from an emerging labour market in neighbouring urban centres (Kaplan 1996). Furthermore, in the context of increasing completed family sizes and of land shortages, education may also be seen as a new opportunity for resource diversification in tap villages. In a focus group discussion, one villager reported, *'If my children were not educated, they would live with me. But I don't have enough farming land, so I would have had a tough problem. Thanks to education [they should find jobs and] I am free from the problem'.*

There is also evidence that the introduction of water taps is associated with increased competition between siblings for education. Despite the overall increases in the probability of receiving formal education, this resource was distributed less equally within households in tap villages. In tap villages, parents invested more in educating early-born children at the expense of their later-born offspring. In raw percentages, 51 % of first births attended school in tap villages, dropping to 25 % for later-born children (8+birth order). In non-tap villages, birth order was less important; around a third of children at any birth order attended school (Gibson and Lawson 2011). These results suggest that Arsi Oromo parents who experienced the lower rates of child mortality due to improved water supplies concentrated educa-

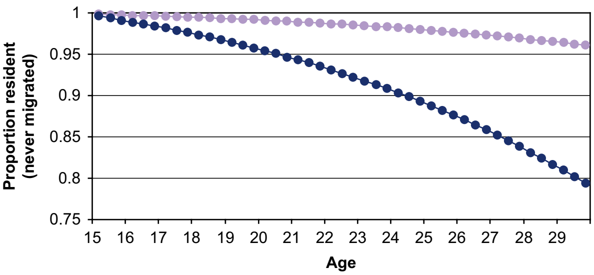


Fig. 4.6 Kaplan–Meier/survival plot of timing of outmigration (cumulative probability; with taps: *light font*, without taps: *dark font*)

tional investment on their first-born child, leaving later-born children uneducated to assist with farming activities. Conversely, under conditions of high extrinsic risk to health (as found in the non-tap villages), parents spread this investment more equally among their offspring, perhaps because they could not predict which child would survive, and therefore which would be economically successful (Liddell et al. 2003). It has been argued that such biases between siblings may be magnified during early stages of 'modernisation' and 'urbanisation' where competition between individuals for limited but profitable jobs requiring formal education is most acute (Eloundou-enyegue and Williams 2006).

4.3.5 Migration

The installation of tap stands has fuelled increased outmigration of young adults (15–30 years) to nearby urban centres (Fig. 4.6). The main stated reason for outmigration was seeking high school education (75 %) or employment in casual wage-labour jobs (13 %) in nearby towns. In hazards regression models, young adults gaining access to taps had twice the odds of migrating out by the age of 30 than their peers living without taps (Gibson and Gurmu 2012). We have argued that this was fuelled by increases in family sizes linked directly with improved water supplies, which have reduced child mortality and increased fertility. In addition, secular changes arising simultaneously with development intervention may have contributed to a more positive cultural outlook on migration and aspirations of 'modernity'.

Under conditions of population growth, outmigration of young adults may be one strategy to alleviate the harmful effects of increasing resource competition for locally limited food and heritable resources (such as agricultural land and marriage opportunities). This finding is supported by evidence that family dynamics strongly predicted the timing of outmigration (Gibson and Gurmu 2012). The birth of a younger sibling doubled the odds of a young adult migrating out to an urban centre. Males, who compete for heritable land, were particularly sensitive to family effects. Large numbers of siblings were an important determinant of male outmigration. Among 739 households with eight or more siblings, 24.4 % of males had left for urban centres, whereas among households with less than four siblings, this figure dropped to 6 %. For Arsi Oromo females, migration was less common due to their domestic responsibilities, most notably caring for younger siblings (24 % of males versus 12.1 % of females aged 15–30 years had ever migrated out).

Levels of migration for the Arsi Oromo were low. In 2009, few young adults had ever migrated out (15.5 %), and urban residence was temporary (most staying less than a year). Focus group discussions revealed divided local opinions on the benefits of outmigration (for details, see Gibson and Gurmu 2012). Costs were viewed in terms of the financial hardships which migrants encounter in the city, difficulties finding paid jobs (the average migrant sent home less than US$ 50 per month) and risks encountered through theft and sexual exploitation. However, new urban livelihood opportunities, e.g. in labour construction industry and domestic service were also perceived by many Arsi Oromo as realistic and attractive employment alternatives to farming. Given a continued decline in the ratio of agricultural land to people, reduced agricultural productivity and nationwide improvements to communication links and urban economic development, it seems likely that the pace and scale of rural to urban migration from this community will accelerate in the future (Gibson and Gurmu 2012).

4.4 Discussion

Economist Esther Boserup (1965) predicted that population growth should spur human technological invention that keeps supply ahead of demand. This chapter has identified the reverse, a situation where technological invention may actually have exacerbated rather than alleviate population pressures (at least in the short term). Investigations have revealed that a labour-saving rural development project has had a dramatic impact on community health and social welfare for the Arsi Oromo (summarised in Table 4.2). It has introduced substantial improvements to women's lives, reducing the time and effort that they spend carrying water on their backs (from 6 h a day to less than 30 min in some instances) and improving child survival (reducing the relative risk of child death by 50 % for every month of life). However, the development project has also introduced striking and unexpected demographic consequences. Access to water taps has been linked to an immediate increase in female reproductive rates, supporting an evolutionary life history prediction that improvements in women's energy budgets would translate into higher fertility. Women who gained access to taps had shorter birth intervals (triple the odds of child birth per month) than those women without access to taps. Combined with increased child survival, brought about by improved water supplies, this has underpinned increases in family sizes in a population close to environmental limits under current technology.

A critical outcome of this long-term field study has been the revelation of how development without family planning and/or incentives for reducing family size may fuel Malthusian consequences in poor households (summarised in Table 4.2). In the absence of adequate food supplies, poorer maternal body condition for Arsi Oromo women was evident due to the energetic costs of high fertility. Further, increases in levels of child malnutrition in tap villages may have occurred as parents struggle to feed larger numbers of surviving offspring (Weaver and Beckerleg 1993). The Malthusian concern that population growth will outstrip the potential for food production (Malthus 1798) currently appears to retain its relevance not only for the Arsi Oromo, but also for other communities in the region. Ethiopia is the fifth fastest-growing country in Africa, with a population size expected to double to 173 million by 2050 (United Nations 2011). Over a third of the population are undernourished and one-fifth are dependent on humanitarian aid (FAO 2012). Here, the combined effects of rapid population growth, climate change and dependency on agriculture are posing a grave threat to food security and well-being (Alexandratos 2005).

Development and the population pressures it has fuelled have also influenced education and livelihood practices among the Arsi Oromo. Scarcity of farmland has driven a trend towards resource diversification (increased investment in education and higher levels of rural–urban migration in search of alternative income-generating opportunities which are not available locally). However, the benefits associated with increased education are not shared equally among offspring. In the analyses described here, parents with access to development intervention invested more in their offspring's education than those in non-tap villages, but preferentially in first-born male offspring. A pattern that may be driven by increased certainty in the returns to investment following reductions in child mortality. Young adults gaining access to development were also more likely to migrate to urban centres in search of new opportunities for advanced training and more lucrative off-farm employment.

On first consideration, improved outmigration to urban centres might appear a beneficial strategy for both the individual and the rural household. Cities generate jobs and income, deliver education, health care and other services more efficiently than less densely settled areas, simply because of their advantages of scale and proximity (UNFPA-Technical Division 2012). Outmigration and resource diversification should reduce rural population pressures, land shortage and environmental degradation, while substantial remittances may flow from urban to rural communities, making a more sustainable alternative to rural development aid (Gupta et al. 2009). However, in Ethiopia the scale and pace of urban expansion are currently unsustainable. Government statistics indicate that 50 % of the urban population are landless migrants from rural areas (Central Statistical Agency [Ethiopia] 1998). And the jobs and services are not available to sustain this migrant community: A third of urban residents are unemployed, and 80 % live in substandard housing (UN-HABITAT 2008). For the Arsi Oromo, there are currently few financial benefits of moving to urban centres; remittances are small and most young migrant adults return to the villages within a year empty-handed (Gibson and Gurmu 2012). Like many of the region's poorest communities, rapid urbanisation is increasingly concentrating poverty, creating strain on infrastructure and public services (UN-HABITAT 2008; Byass et al. 2003).

An evolutionary approach, however, may indicate that over the longer term, rapid rural growth, education and urbanisation will lead to further population changes, including smaller family sizes. Urbanisation may speed up fertility decline, as the rising cost of raising successful children in a competitive urban skills-based economy should drive parents to invest more resources in fewer offspring (Mace 2008; Kaplan 1996). Supportive of this assumption, female migrants to Addis Ababa delayed reproduction and limited their fertility in response to the higher cost of urban living (Gurmu and Mace 2008). Resource shortages in rural areas should drive a similar preference for smaller families (Alvergne et al. 2013). Recent evidence from rural Arsi suggests that attitudes to large family sizes are indeed changing, with a growing demand for modern contraceptives—uptake has increased from < 1 to 19 % over the past 10 years (Gibson 2002; Alvergne et al. 2011). However, like many women across the developing world, Arsi Oromo women have an 'unmet need' for family planning. A recent survey identified that one in four Ethiopian women wishes to prevent or delay pregnancy but is not using an effective method of contraception (Central Statistical Agency [Ethiopia], & ICF International 2012). In the absence of adequate contraception, rural development which improves health may be contributing to rather than relieving population pressures on their households and the wider community (Gibson and Mace 2006).

4.4.1 Implications for Policymakers

The findings reviewed in this chapter have clear relevance for the development policymakers and users, who seek to design and evaluate intervention in resource-limited contexts. Identifying that development which fuels population growth (through increased fertility and improved child survival) may also place additional pressure on already stretched rural households as well as community public health services in villages, towns and cities. A key message from this research is that interventions which impact in any way on women's energetic expenditure or increase energy availability should routinely include family planning and reproductive services. At a minimum, initiatives based in low-income settings should include an assessment of the unmet need for family planning and the latent desire for children. This not only follows directly from a life history theory framework, but also supports the longer-term recognition by population policymakers of the need for the integration of family planning with maternal-child health services (Royal Society 2012). At a relatively low cost, these considerations may introduce a range of benefits to the household, the community and the nation. Fewer pregnancies should mean fewer maternal deaths—more than a third are due to unintended pregnancies, in part because of unsafe abortions (Bongaarts and Sinding 2011). Slower growth in the number of children permits more investment in quality rather than quantity in health care and education. Smaller family sizes allow women to join the labour market and enhance women's earnings and autonomy (Canning and Schultz 2012). At a macroeconomic level, it reduces youth dependency, job competition and its wage-depressing effect, and makes it easier for societies to address environmental problems arising from high consumption and environmental degradation (a review on the relationship between population growth and economic development can be found in the report on population and the environment published by the Royal Society in 2012). Finally, it is cost-effective. The UN estimates that 'for every dollar spent in family planning, between 2 and 6 $ can be saved in intervention aimed at achieving other development goals' (United Nations 2009).

The dramatic population changes linked with development described here also could help to explain why many countries in Africa have not experienced the rapid transition to low fertility ('the demographic transition'), which occurred in Europe a century earlier. Country-level statistics suggest that during demographic transitions, countries undergoing mortality declines do experience an initial rise in birth rates prior to a long-term decline in fertility (Dyson and Murphy 1985). However, in most of these cases the reduction in mortality has arisen from endogenous, gradual economic development and technological advancement (Coale and Watkins 1986). Our findings suggest that where mortality decline is brought about by external intervention, in the absence of general economic improvement, the transition to low fertility may follow a different pattern. Further, in predominantly rural countries, where jobs and reliable medical and contraceptive supplies are in short supply, the process may be much slower.

This investigation also raises several questions concerning the best way to monitor the effectiveness of development. For example, is there an appropriate end point for development evaluation? NGOs often move on to new projects once their short-term practical objectives have been achieved; however, this case study has revealed that the demographic consequences of tap installation have been far-reaching. Linked to this is the question of whether NGOs need to have greater engagement with anthropological scientists, who can generate testable theoretical predictions regarding long-term consequences of intervention, and also contribute new data collection and analytical methods (see introductory chapter of this book). Efforts to evaluate development interventions are often overly narrow and rarely driven by theory, which has limited a full accounting of the costs and benefits. The chapters in this volume testify to a growing body of research grounded in evolutionary theory, revealing how imperative these considerations should be.

Population growth, dependency on aid, environmental degradation and unplanned urban growth have been highlighted as the main factors impeding sustainable social and economic development (UNFPA-Technical Division 2012). While disentangling these effects may not be easy (Dyson 2011); evolutionary science, particularly human behavioural ecology may have much to contribute to this endeavour (Nettle et al. 2013). The main finding of the case study presented here, that improving health conditions (via labour-saving development technology) can introduce positive but also potentially dangerous impacts on the local population, has been recognised by others; however, it is the evolutionary theory which provides a mechanism that allows us to disaggregate how and why this might be.

Finally, if the key challenges of the twenty-first century relate to population pressures, we need to develop a better understanding of the relationship between demography and development, particularly in countries with fewer resources and slower rates of economic growth. For both evolutionary and non-evolutionary scientists, "paying attention to demographic indicators and acting proactively on their determinants and consequences offers considerable potential to promote human well-being" (Bloom 2011).

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Part II
Family Structure & Reproduction

Chapter 5
Family Structure and Health in the Developing World: What Can Evolutionary Anthropology Contribute to Population Health Science?

David W. Lawson and Caroline Uggla

Abstract In this chapter, we consider what evolutionary anthropology contributes to the study of population health, focusing specifically on family structure and its relationship to child and adult physical health. Evolutionary anthropologists have now built a substantial body of literature on relationships between family structure and various dimensions of human wellbeing, particularly in the context of small-scale 'traditional' societies and developing rural communities most at risk of poor health outcomes. Crucially, they have also constructed theoretical models to account for variation in key dimensions of family structure in relation to individual, ecological, and cultural factors. Thus, evolutionary anthropologists have much to say, not only about the extent to which specific family structures may influence health but also why certain family forms may persist or change across time and space. Here, focusing on studies primarily conducted in sub-Saharan Africa, we review the literature on three interrelated dimensions of family structure and their relationship to health: (1) family size, (2) polygynous versus monogamous marriage, and (3) the role of extended kin. Using these examples, we highlight the theoretical and empirical contributions of evolutionary anthropology and draw out implications for population policy and related initiatives seeking to improve family health in the developing world.

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5.1 Introduction

Evolutionary anthropology has much to offer population health science, both as a rich and integrative theoretical framework and as an active producer of a now substantial body of relevant empirical literature. Here, we focus specifically on the study of family structure and its relationship to child and adult physical health in the developing world. Family and health are intimately tied. Family formation defines residence and relatedness, and so fundamentally determines patterns of resource production, allocation, and consumption. The family is also a key site for navigating conflicts of interest between individuals, including not only conflicts between consumers over limited resources but also conflicts between generations, between the sexes, and with and between extended kin, which often have different priorities to individuals within the nuclear family. All of these factors mean that family structure is anticipated to influence health. Health is also one of the many factors that determine the assortment of individuals into particular family structure types. Healthier individuals, for example, find it easier to reproduce successfully, are more likely to survive to old age, are more attractive as marriage partners, and are more able to assert their own autonomy or dominance when conflicts of interest arise. This bidirectional relationship between family structure and health represents an important research theme we return to throughout the chapter.

Population heath science can be defined broadly as the study of health inequality within and between populations, including health outcomes, health determinants, and the design and critique of measures that may be taken to improve health and reduce inequality (Kindig and Stoddart 2003; Young 2005). Key to this perspective is the focus on health variation in the population as a whole, rather than considering only ill or high-risk individuals. Researchers working under this umbrella definition may also identify themselves variously as (social) epidemiologists, demographers, or economists, and, although there is a shared commitment to identifying both barriers and practical solutions for improving human wellbeing, there is no single overarching theoretical framework. While a range of methodologies are used, population health is most often studied through the analysis of large, systematically collected and representative data sets, such as censuses, cohort, and panel studies (David and Haberlen 2005). In the case of family structure and health in developing countries, a frequent source of information is the Demographic and Health Surveys (DHS)—national cross-sectional surveys carried out at regular intervals since the 1980s and funded primarily by the US Agency for International Development (www.measuredhs.com). Such data sets have a number of strengths; sample sizes are large, a broad range of information is collected, and surveys use a standardized questionnaire and protocols to facilitate comparative analysis. However, as we shall discuss, analyses of large-scale surveys such as the DHS often suffer important limitations.

Evolutionary anthropology in contrast is concerned with explicitly evolutionary models of human variation, including variation in both family structure and physical health. Its practitioners are committed to a more or less unified theoretical framework that considers the diversity of human behaviour as reflective of plastic evolved solutions to problems posed by local physical and social environments across human history (Brown et al. 2011; Nettle et al. 2013; Winterhalder and Smith 2000). Research is thus primarily motivated by the elaboration and evaluation of alternative hypotheses regarding human adaptation. In this sense, evolutionary anthropology takes a 'top-down' approach to research, whereby the general theoretical principles of evolutionary biology are used to generate hypotheses that guide the study of specific phenomena. This contrasts with the 'bottom-up' approach more typical of population health science, which begins with the description of a particular health issue, which then may or may not lead to the generation or modification of a broader theoretical model to account for observed relationships, often in a piecemeal fashion. Furthermore, evolutionary models uniquely consider *ultimate causation,* i.e. explanations for behaviour grounded in terms of evolutionary history and adaptive function. This adds an additional and complementary layer of explanation to the consideration of *proximate causation* more characteristic of the social sciences, i.e. explanations grounded in the assumed properties of human physiology, psychology, and culture that do not simultaneously consider the origin and potential function of those properties (see Mayr 1961; Tinbergen 1963).

As a branch of anthropology, evolutionary anthropological research is usually carried out at the level of specific communities and well-defined cultural contexts, often focusing on the collection of data from populations where subsistence relies heavily on foraging, pastoralism, or small-scale agriculture. Such 'traditional populations' are often marginalised by population health scientists working in the developing world, where attention is more generously devoted to collecting and analysing data that are generalizable to the majority (i.e. typically nation states or culturally heterogeneous regional units). Thus, as Rende Taylor (2005) emphasizes, evolutionary anthropological studies are often particularly valuable in that they often combine both meaningful quantitative analysis, lacking in purely ethnographic studies in social anthropology, with a more nuanced interpretation at the family and community level that large-scale demographic studies rarely provide. It should be noted that not all quantitative research in anthropology is evolutionary, and in this respect the contributions of evolutionary anthropology blur with overlapping research traditions in biosocial anthropology (Panter-Brick and Fuentes 2009; Stevenson and Worthman 2013) and anthropological demography (Kertzer and Fricke 1997). Furthermore, while primary data collection from small-scale rural populations remains at the heart of evolutionary anthropology, increasingly researchers are incorporating analyses of secondary demographic data sets to address evolutionary questions (e.g. Goodman et al. 2012; Nettle and Pollet 2008; Lawson et al. 2012). This development is particularly welcome, because the use of similar sources of data undoubtedly encourages exchange between disciplines.

With these points in mind, the chapter is structured as follows. We first briefly characterize how evolutionary anthropologists view family structure within the broad comparative perspective of evolutionary biology. We then review how evolutionary anthropologists currently understand variation in family structure and its predicted relationships with the physical health of family members across three interrelated dimensions: (1) family size, (2) polygynous versus monogamous marriage, and (3) the role of extended kin. For each of these dimensions, we consider how available data stack up against the predictive framework of evolutionary anthropology. We then reflect on the implications for population policy. These implications are not always unique to an evolutionary perspective, but rather drawn on important points of emphasis within the literature. We focus primarily on child and, to a lesser extent, maternal health, but consider adult male health where data are available. Our aim is to illustrate the theoretical and empirical contributions of evolutionary anthropology and to provide a general synthesis of the current literature, rather than conduct a fully exhaustive review. We make reference to more thorough reviews where possible and point out key issues of debate where they exist.

5.2 An Evolutionary View on the Human Family

Evolutionary anthropologists approach the study of the human family from the perspective of one or more of the three main cornerstones of evolutionary biology: (a) *life history,* (b) *sexual selection,* and (c) *altruism* (see Box 5.1). In all cases, research, first and foremost, takes an optimality approach to understanding behaviour (Parker and Maynard Smith 1990). This is because natural selection shapes the behaviour of all organisms in response to the pay-offs experienced to alternative behavioural 'strategies' across evolutionary history. This assumption, that human behaviour can be understood as functionally tied to the costs and benefits of action, brings evolutionary thinking very close to the principle of 'utility maximization' in economics (Nettle et al. 2013). However, an evolutionary perspective is distinct in at least two important ways.

Box 5.1 Theoretical cornerstones of evolutionary biology

a. Life history theory

Life history theory concerns the scheduling of events that describe an organism's life cycle, e.g. age at sexual maturity, and the number and timing of births (Roff 2002; Stearns 1992). Observed life histories are constrained by the general principle that resources (time, energy, effort) allocated to one function cannot be allocated to another. Thus, natural selection acts to optimise fundamental life history 'trade-offs', including trade-offs between investing in reproduction versus somatic maintenance, between investing in mating versus parental effort, and between investing in offspring quantity versus quality (see Sect. 5.3). Human life history is remarkable among primates in a number of regards, including an extended juvenile period, high fertility and longevity relative to our body size, and the evolution of menopause (for comprehensive reviews, see Bribiescas et al. 2012; Kaplan et al. 2000; Lawson 2011; Mace 2000). Human life history also displays extensive phenotypic range, with patterns of mating, reproduction, and parenting varying dramatically both within and between populations (Lawson and Mace 2011; Low 2007). A key aim of life history studies is therefore to consider whether or not this diversity can be understood as reflecting adaptive variation in resource allocation.

b. Sexual Selection

Sexual selection concerns the evolution of strategies to obtain and copulate with mates (Darwin 1871). As mammals, humans are characterized by internal gestation and lactation, and so the physiological aspects of parental investment are heavily weighted towards females. Trivers (1972) predicted that females thus represent a limiting resource with respect to male fitness and sexual selection will lead to high levels of intrasexual competition between males for access to females, while females will place relatively more emphasis on assessing the quality of potential reproductive partners. Recent theoretical reformulations however question the assumption that initial asymmetries in parental care predispose such sex roles and place emphasis on contextual factors such as local mate availability, variation in mate quality, and the costs associated with seeking new mates (Kokko and Jennions 2008). Reproductive behaviours of both sexes are seen as strategic and in response to the future pay-offs of a particular behaviour as opposed to being driven by past investment (sunken-cost fallacy; Dawkins and Carlisle 1976). Further complexity arises in humans because relationships between mating and reproductive success appear highly variable between cultures (reviewed in Brown et al. 2009). Nevertheless, understanding the different constraints and priorities of the sexes remains central to evolutionary models of human mating and marriage (see Sect. 5.4). An additional concern is the role of sexual conflict, i.e. the evolution of strategies to gain the upper hand when the interests of the sexes differ (Aloise et al. 2013; Borgerhoff et al. 2009). There is considerable anthropological evidence of male strategies to restrict female sexuality in particular, and since males typically exert more control over resources, there is good reason to believe sexual conflicts may often be resolved in the favour of men (Smuts 1995).

c. Altruism

Finally, models of *altruism* are of crucial importance to evolutionary studies of the family. Most importantly, altruism is predicted to be high between close genetic relatives (Hamilton 1964), explaining the evolution of parental care, but also the fact that kinship represents a universal feature of human social organization (Shenk and Mattison 2011). However, relationships between different categories of kin are not equal. More genetically distant relatives are predicted to more rarely engage in altruistic actions, and indeed several studies confirm that the degree of genetic relatedness is a robust independent predictor of social and financial investments between kin (Bowles and Posel 2005; Gurven et al. 2000, 2002; Pollet 2007). Furthermore, the certainty of relatedness between kin may vary in important ways. Thus, fathers and paternal kin are predicted to invest more in children when confidence of paternity is high (Sect. 5.5). High rates of altruism are also anticipated in situations of mutual gain, including most obviously relationships between husbands and (co)wives, who share interests in cooperatively raising offspring, and in situations of both direct and indirect reciprocity (Trivers 1971). Indeed, the extent of cooperation between non-kin is extreme in humans, leading to much debate about the evolutionary mechanisms at play (Fehr and Fischbacher 2003; Henrich 2004; Lamba and Mace 2011).

Firstly, evolution by natural selection provides a grounding logic of why humans are predicted to behave optimally in the first place, a starting assumption that is taken for granted by economists. Moreover, evolutionary models anticipate that behaviour is deployed in the service of inclusive fitness, i.e. production of long-term genetic descendants, rather than physical or mental health, financial prudence, or other measures of personal or societal wellbeing (Hill 1993). Thus, an evolutionary perspective provides conceptual clarity with regard to what currency behaviour is predicted to be ultimately optimising (i.e. the 'utility' of behaviour). This observation has obvious immediate relevance to studies of population health. Supporting the view that humans generally behave in ways that maximize their inclusive fitness, positive correlations between indicators of 'cultural success' (e.g. social status, wealth) and reproductive success are a common feature of natural fertility populations (for evidence and discussion, see Borgerhoff Mulder 1987; Nettle and Pollet 2008).

The second important distinction is that, through consideration of the inherently imperfect proximate mechanisms of adaptation, evolutionary approaches also provide us with expectations about when we should expect departures from optimality. It is useful to consider three broad interrelated categories of adaptive mechanisms: *physiological, psychological,* and *cultural*. For example, the automatic suppression of ovulation when a woman is breastfeeding is widely understood as a physiological adaptation to avoid pregnancy at times when it could risk maternal or child survival (Ellison 1990). Likewise, family formation may be guided by evolved psychological mechanisms whereby motivations for child rearing subconsciously or consciously respond to environmental cues, such as local mortality risk (e.g. Mathews and Sear 2008; Nettle 2011) or the impact of reproduction on own or descendant socioeconomic success (Goodman et al. 2012; Kaplan and Gangestad 2005). Finally, humans undoubtedly rely heavily on socially learned information. Studies of 'cultural evolution' consider our reliance on differential social learning rules, such as tendencies to copy the most frequent behaviours ('conformity bias') or the behaviours of those deemed most successful ('prestige bias'). Transmitted culture may also introduce new behavioural variants to a population, which may spread within and across generations and evolve semi-independently of genetic or environmental influences (Brown et al. 2011; Mesoudi 2011; Richerson and Boyd 2008).

The specifics of these evolved 'decision-making' mechanisms can be considered imperfect because they are shaped by energetic, developmental, and phylogenetic (i.e. historical) constraints, limiting the option set of potential strategies available to the human organism. As natural selection effectively adapts behaviour to past, not present environments, mechanisms of adaptation are also predicted to deal somewhat poorly with environmental novelty resulting from rapid social or ecological change (Irons 1998; but see Laland and Brown 2006). Constraints aside, the results of optimality modelling are also dependent on the accurate conceptualisation of the pay-offs to alternative behaviours within environments and the degree of overlapping or conflicting interests between individuals (e.g. Borgerhoff Mulder and Rauch 2009). Thus, it is important to emphasize that evolutionary thinking rarely gives rise to single or obvious explanations for human behavioural diversity (Brown et al. 2011). Recognizing this fact, evolutionary anthropology is a rigorously empirical discipline, placing much value on testing competing predictions against available data. Since data on long-term inclusive fitness are often difficult to collect, much of this research makes use of more immediate proxies including fertility, child survival, and physical health, leading to much overlap with the population health literature.

5.3 Family Size

Human fertility (number of births), and consequently family size (number of living children/siblings), is highly variable, both between and within populations. Total fertility rates average around four to six for contemporary hunter-gatherers (Kelly 1995). Shifts to agriculture are generally associated with higher fertility and also improved child survival (Bentley et al. 2001; Sellen and Mace 1997, 1999). At the extremes, a population average of more than ten births per women has been recorded (Eaton and Mayer 1953). However, all forms of rural subsistence demonstrate a high degree of heterogeneity in demographic parameters (Randall 2008; Sellen and Mace 1997, 1999). At the global level, child mortality has declined substantially in recent decades, but fertility rates have dropped more slowly, particularly in sub-Saharan Africa leading to unprecedented population growth (Lee 2003). Indeed, the population of sub-Saharan Africa is set to double from 0.86 to 1.96 billion between 2010 and 2050 with some countries (e.g. Niger) tripling in size (Ezeh et al. 2012). This growth is generally viewed as having adverse consequences on population health via increased pressure on public services and infrastructure, a high ratio of young to working-age people, increases in maternal and child mortality, and environmental degradation. Consequently, much population policy in the developing world concerns effort to encourage lower fertility, primarily through expanding the uptake of modern contraceptive technologies (Bongaarts 1994; Ezeh et al. 2012; Schultz 2007).

Evolutionary anthropologists have studied both the ultimate causes and proximate mechanisms regulating human fertility and family size, primarily taking a life history perspective (see Box 5.1a). Thus, variation in reproductive behaviour is understood as the resolution of resource allocation trade-offs between reproduction and competing domains such as growth, survival, and the care of offspring (Kaplan et al. 2002; Kaplan 1996; Lawson and Mace 2011). This framework overlaps considerably with economic models of fertility which also emphasize the opportunity costs of reproduction, trade-offs between offspring quantity and quality, and resource flow between generations (Becker 1981; Caldwell 2005; Kaplan 1994), but also integrates more broadly with a consideration of physiological and cultural factors. Below, we review the evidence that fertility influences parental and child health, before discussing how evolutionary anthropologists account for variation in fertility, including the dramatic decline in fertility rates associated with population social and economic modernisation, i.e. the so-called demographic transition (Lee 2003; Borgerhoff Mulder 1998).

5.3.1 Trade-Offs Between Reproduction and Health

It is well recognized by population scientists that the ability to conceive and successfully complete a pregnancy is closely dependent on a woman's physical health, which therefore acts an important proximate determinant of variation in fertility, at least within the developing world (Bongaarts 1978). From an evolutionary perspective, this also represents the adaptive resolution of the life history trade-off between reproduction and survival, with resources automatically allocated to somatic maintenance over reproduction when energy is in short supply (Bentley 1999; Ellison 1990). Further evidence that fertility is traded off against maternal health also comes from studies reporting negative correlations between fertility and female longevity (e.g. Gagnon et al. 2009). However, since women need to be healthy to reproduce, those with the highest fertility are often healthier to begin with, and so studies of this kind often suffer from issues of statistical confounding. Perhaps unsurprisingly then, not all studies have detected the hypothetical 'costs of reproduction' (Le Bourg 2007; Sear 2007). Additional research has focused on twinning as a more exogenous measure of fertility, where it is associated with not only an increased risk of maternal death in childbirth but also reduced post-reproductive survival of mothers (Gabler and Voland 1994; Helle et al. 2004; Sear 2007). Likewise, several studies report that mothers who have relatively more sons than daughters are likely to die younger (e.g. Helle et al. 2002; but see Beise and Voland 2002), an effect that has been attributed to a greater physiological cost of carrying male foetuses to term. Thus, overall, while difficult to quantify, there is good evidence that high fertility can reduce maternal health, and that such costs are consequently an important determinant of fertility patterns, particularly in contexts where modern forms of contraception and/or alternative motivations for limited fertility are absent.

Whether or not reproduction has costs to paternal health has less often been studied, and indeed is not anticipated since the physiological costs of reproduction fall on females. In fact, recent evolutionary studies have suggested that reproduction may have positive impacts on male health via more subtle hormonal mechanisms. Testosterone is proposed to mediate resource allocation to mating versus parenting investment in humans and other species, so that males who focus on the mating effort are predicted to maintain elevated testosterone, whereas males who cooperate with a female partner to care for offspring are predicted to reduce testosterone production (Hirschenhauser and Oliveira 2006; Wingfield et al. 1990). Supporting this proposal, testosterone levels have been found to be lower among partnered men compared to single men, and that the transition to fatherhood is associated with a further reduction in testosterone levels (Alvergne et al. 2009a; Gettler et al. 2011; Gray et al. 2002; Muller et al. 2009). Testosterone production is also an immunosuppressant, elevates risks of prostate cancer, and is linked to an increased likelihood of risky behaviour, including alcohol and drug use, at least within Western contexts (e.g. Dabbs and Morris 1990; Parsons et al. 2005). As a result, while healthier men are more likely to marry and have children, a reduction in testosterone levels following family formation may also partially explain why fathers and partnered men are often healthier within populations (Gettler et al. 2011).

5.3.2 *Trade-Offs Between Offspring Quantity and Quality*

Evolutionary anthropologists have conducted much research aiming to test the prediction that, all else being equal, larger family size will disadvantage children because it dictates a dilution of individual shares of parental investment. From a life history theory perspective, parents are anticipated to tolerate such costs because inclusive fitness is maximized by the total, rather than individual, contribution of each offspring to the pool of future descendants (Roff 2002; Stearns 1992). Table 5.1 summarizes the results of prominent studies by evolutionary researchers estimating the effect of family size on child growth or child survival (see also Blurton Jones 1986, on optimal birth spacing). These studies are mostly carried out within specific communities/cultural contexts, rather than based on large-scale national surveys (but see Lawson et al. 2012). Overall, many studies present evidence of a trade-off between offspring quantity and quality in the domain of child health. Yet, in a significant number of studies predicted relationships are absent, and effect magnitude varies between studies (see also Lawson and Mace 2011). Variation between studies may result from issues of residual statistical confounding since in many populations the wealthiest families are also typically the largest. On the other hand, not all studies exclude reverse causality. In particular, fertility–child survival relationships may also be established by ‘replacement’ or ‘insurance’ effects, whereby a mother has additional births to compensate for earlier infant death(s), or expected deaths in the face of predicted extrinsic mortality. As such, the costs of high fertility/large family size are likely to be overestimated in some analyses (Lawson et al. 2012).

Table 5.1 Estimated effect of family size (or close proxy thereof) on child health

Population[a]	Child health outcome		Notes	References
	Growth	Survival		
!Kung of Botswana	n.a.	–		Pennington and Harpending 1988
18th–19th-century Germany	n.a.	↓/–	No. of same-sex siblings reduces infant survival in children of farmers, but not in landless labourers	Voland and Dunbar 1995
Aché of Paraguay	n.a.	↓/–	No. of siblings reduces survival between ages of 5 and 9 years, but not under 5 years	Hill and Hurtado 1996
Dogon of Mali	n.a.	↓		Strassmann and Gillespie 2002
	↓	↓		Strassmann 2011
Shuar of Ecuador	↓	n.a.		Hagen et al. 2006
Rural Gambians	n.a.	↓		Mace 2007
Kipsigis of Kenya	n.a.	↓/–	Negative or n-shaped relationship of no. of brothers to survival to 5 years depending on model specification	Borgerhoff Mulder 2007
19th-century N. America	n.a.	↓		Penn and Smith 2007
18th–19th-century Finland	n.a.	↓		Gillespie et al. 2008
Bimoba and Kusasi of Ghana	n.a.	↓		Meij et al. 2009
Sub-Saharan Africa	n.a.	↓/–	Negative effect in all countries, but significant variation in magnitude both between and within countries	Lawson et al. 2012

[a] This table includes only studies specifically addressing the predicted offspring quantity–quality trade-offs from an evolutionary perspective. It does not represent a complete survey of the literature on family size and child health

Key: – no relationship, ↓ negative relationship, ↑ positive relationship, / relationship varies by subgroup (see Notes column for details); *n.a.* not applicable, i.e. study did not explore this outcome

Variation in the magnitude of trade-off effects between studies may also reflect context dependency. For example, quantity–quality trade-offs will logically be weaker when the local determinants of offspring quality are predominantly ‘extrinsic’, i.e. independent of variation in levels of parental investment (Gibson and Lawson 2011; Pennington and Harpending 1988; Quinlan 2007). In the context of many traditional populations, extrinsic risks to health and survival are predicted to be high because environmental factors limit parental ability to protect offspring, including unavoidably high pathogen loads, poor sanitation and health-care access, and significant vulnerabilities to subsistence failure, natural disasters, and violent conflict.

Supporting this assessment, Lawson et al. (2012), through analysis of African DHS, conclude that the cost of high fertility, as estimated by the relative decrease in the odds of child survival per additional birth, tends to be weaker in contexts where child mortality is initially already high due to other factors. Similarly, Desai (1995) reports that having a close-aged sibling is more likely to be associated with poor child health in developing countries with better clean water supply or health service access, suggesting that without these resources parents have limited ability to protect their children through increased investment per child. Such large-scale analyses are undeniably crude in that they lack direct data on associations between parental care and child outcomes, but there is also supporting qualitative evidence that parents in resource-poor settings perceive child deaths and illness to be a largely unavoidable part of life (e.g. Hampshire et al. 2009).

Evolutionary anthropologists also recognize that trade-offs between offspring quantity and 'quality' will be influenced by the extent to which children are reliant exclusively on parents. For example, competition between siblings may be reduced when extended kin share the burden of childcare, particularly when such help is given in proportion to need (Sear and Mace 2008, Sect. 5.5). In many societies, children themselves may also offset parental costs of child rearing by directly contributing to subsistence activities or alloparental care (Kramer 2005). However, in general, anthropological studies of food production and consumption have concluded that the net transfer of resources over the life course flows strictly from parents to offspring (Kaplan 1994; Lee and Kramer 2002). This contradicts the persistent view of some demographers that, within much of the developing world, having children is more likely to present a net economic asset to parents (for discussion, see Caldwell 2005).

5.3.3 Optimising Family Size

With family size influencing not only maternal but also child health, a final question to consider is the extent to which fertility rates can be understood as adapted to environmental variation. In addressing this question, many studies have focused on the trade-off between fertility and child survival (e.g. Lawson et al. 2012; Meij et al. 2009; Strassmann and Gillespie 2002). This is because child mortality represents a selective bottleneck in human evolution, i.e. many offspring fail to survive the first 5 years of life, but if they do so they are very likely to reach adulthood (Jones 2009; Mace 2000). Furthermore, while there is evidence of later reproductive competition between those that survive childhood, particularly among brothers over marital placements (Borgerhoff Mulder 2000; Gibson and Gurmu 2011; Mace 1996), such effects are not universal (Gibson and Gurmu 2011; Lawson and Mace 2011) and are more often associated with high fertility and biased inheritance systems, rather than reduced fertility (Hrdy and Judge 1993). In a review of the literature, Lawson et al. (2012) argue that the cost of fertility on child survival alone is not sufficient to motivate the limitation of reproduction even at the highest fertility levels. Thus, trade-offs between fertility and maternal somatic maintenance, rather than child survival, may be more important in determining variation of pre-demographic transition fertility levels. This conclusion is also consistent with classic demographic accounts of natural fertility, which give primacy to physiological mechanisms such as lactational amenorrhoea, and contend that reproduction in pre-demographic transition societies is rarely (consciously) strategic with respect to its effects on children (Bongaarts 1978; Lloyd and Ivanov 1988; van de Walle 1992).

Why fertility rates almost always fall as societies transition from a preindustrial to postindustrial economy is a source of heated debate for both demographers and evolutionary anthropologists (Borgerhoff Mulder 1998; Mason 1997; Shenk et al. 2013). Paralleling the non-evolutionary demographic literature, evolutionary explanations focus alternatively on (1) the rising conflicts between reproduction and economic productivity, particularly for women, and the increasing socioeconomic pay-offs to investing heavily in child education (Kaplan 1996) or (2) shifting patterns of social interaction proposed to modify cultural ideals surrounding reproduction, more or less independently of the costs of child rearing (Newson et al. 2005; Richerson and Boyd 2008). Recent empirical studies suggest that, in general, economic factors provide the best explanation of why fertility falls as populations ‘modernise’ (e.g. Shenk et al. 2013) and that cultural transmission cannot be considered a root cause of preferences for smaller family size because the earliest stages of the transition are inherently reliant on behavioural innovation rather than social diffusion (Alvergne et al. 2011). Modern fertility decline is also clearly maladaptive in an evolutionary sense because those unusual individuals who do have larger families ultimately produce many more long-term genetic descendants (Goodman et al. 2012). Thus, as Kaplan (1996) argues, fertility decline may be best understood as the by-product of evolved, but no longer adaptive mechanisms that motivate human behaviour towards goals of economic and social success (see also Kaplan et al. 2002).

5.3.4 Implications for Policy

1. An evolutionary perspective makes clear from the outset that the mechanisms regulating human reproduction are always likely to tolerate some cost to health in the service of inclusive fitness, and that there will be parent–offspring conflict in ideal reproductive behaviours. Such insight may be useful in improving the design of initiatives aiming to improve family health. For example, building on a conceptual model of evolutionary parent–offspring conflict over breastfeeding decisions, Tully and Ball (2013) argue that public health campaigns will be most successful when mutual benefits to increasing breastfeeding duration for both mother and child are promoted, rather than the child or mother in isolation (see also McDade 2001; Sellen 2007).
2. Variation in fertility in pre-demographic transition societies appears best understood as largely mediated by maternal health. As such, any initiative that

improves maternal wellbeing in resource-poor settings may also inadvertently increase fertility, leading to additional unforeseen negative health consequences as families struggle to care for additional children (Gibson and Mace 2006; Kramer and McMillan 2006). The long-term effectiveness of programmes that improve maternal health may therefore be improved by also integrating family planning and reproductive services (see also Gibson, Chap. 4, this volume).

3. Population policy often assumes that smaller family size will lead to both substantial health and socioeconomic benefits (Bongaarts 1994; Schultz 2007). However, the literature reviewed above also cautions that there is likely to be much context dependency in the health benefits of fertility limitation. Likewise, while high fertility clearly has negative influences on offspring socioeconomic outcomes in modern developed populations (e.g. Goodman et al. 2012), inferring that fertility decline will automatically reap equivalent benefits in the developing world would be erroneous. Indeed, both evolutionary and economic models of the demographic transition understand fertility decline as a response to magnified benefits of low fertility, whereby the effects of family size on human capital generation are conditional on the availability and quality of schools, health facilities, and labour opportunities (Kaplan 1996; for evidence see Maralani 2008). Applied research should prioritise a greater understanding of this context dependency, not only because it greatly influences the projected impact of changes in fertility on population health but also because it may be useful in determining what factors can be targeted to alleviate the costs of large family size where it already exists (e.g. support from kin, child contribution to productive tasks), rather than narrowly focusing effort on the reduction of fertility itself.
4. Finally, policy aimed at reducing fertility in the developing world largely focuses on improving contraception access. Contraception is an important proximate mechanism by which fertility is reduced, but access alone cannot account for why individuals seek to use it, nor why contraceptive use is not ubiquitous even when readily available (see Campbell and Potts 2008 vs. Mace 2008). Evolutionary anthropology's combined focus on proximate mechanisms and ultimate causation of reproductive strategies is therefore instructive. In particular, studies which take an integrated perspective by testing alternative models for the uptake of contraceptive technology may be the most valuable (Alvergne et al. 2011; Alvergne et al. 2013; Borgerhoff Mulder 2009a).

5.4 Polygynous Versus Monogamous Marriage

Polygynous marriage is defined as the marriage of one man to several co-wives, and contrasts with monogamous marriage where a single husband and wife marry. For a recent discussion of polyandrous marriage, i.e. the comparatively rare situation where women marry multiple co-husbands, and its distribution across human societies, see Starkweather and Hames (2012). Polygynous marriage is common cross-culturally, with Murdock and White (1969) estimating that 82 % of preindustrial societies in the ethnographic record allowed men to marry more than one wife. Today, polygynous marriage is most common in sub-Saharan Africa, particularly in West Africa, and is most prevalent in rural areas (Westoff 2003). Within Africa, polygyny is most often nonsororal, i.e. co-wives are not sisters and tend to reside in separate houses; however, in other regions, such as South America, sororal polygyny is more common, and wives typically coreside (White 1988; Winking et al. 2013).

Polygynous marriage is highly relevant to population policy. Its occurrence and legal status has been debated in relation to its potential categorization as a 'harmful traditional practice' argued to infringe on the human rights of women, believed to hold important negative 'emotional and financial consequences' for co-wives and their dependents, and, in some contexts, because it is associated with other harmful practices such as child marriage or female genital mutilation (for recent discussion of these stances, see Gaffney-Rhys 2012; Obonye 2012). Recent large-scale analyses of African DHS data have concluded that polygynous marriage is commonly associated with increased child mortality within countries, bolstering the general view that polygyny is best considered as an important risk factor for poor health (e.g. Amey 2002; Gyimah 2009; Omariba and Boyle 2007). However, rarely do these discussions engage with a consideration of the motivations guiding (male and female) preferences for polygynous marriage. There is also a tendency to prioritise the results of studies based on nationally representative survey data over smaller-scale studies carried out within more specific cultural contexts.

Evolutionary anthropologists have proposed a number of hypotheses for the distribution of human marriage systems across space and time, often embedded in a *sexual selection* framework (Box 5.1b). However, it is important to emphasize from the outset that variation in marriage system generally implies, but does not dictate, patterns of mating and reproduction between the sexes. For example, in populations where serial monogamy is common, men and women may remarry at different rates so that, when the full life course is considered, monogamous marriage equates to polygynous or polyandrous mating (Borgerhoff Mulder 2009b). Furthermore, while monogamous marriage implies that only one wife and her children share resources with a single husband, it does not necessitate that both partners only mate with each other. Indeed, there is considerable historical and ethnographic evidence that, when given the opportunity, men often father children outside of marriage, even in strictly monogamous societies (see references in Fortunato and Archetti 2010). Thus, variation in marriage system may tell us as much about patterns of resource ownership and inheritance as about patterns of sex and reproduction. Below, we introduce alternative evolutionary hypotheses regarding polygynous versus monogamous marriage and by extension how marriage type is anticipated to be associated with health. This section focuses primarily on studies of child health, due to a relative scarcity of studies examining relationships between adult health and polygyny (but see Bove and Valeggia 2009; Sellen 1999). We consider how these models stack up against the empirical evidence from studies examining polygynous marriage within specific communities, rather than across large-scale culturally heterogeneous demographic surveys.

5.4.1 Why Marry a Married Man?

From an evolutionary perspective, it is not hard to understand why men may prefer polygynous marriage, with guaranteed sexual access to additional women enabling higher reproductive success (e.g. Borgerhoff Mulder 1987; Cronk 1991; Gibson and Mace 2007). But female motivations for polygynous marriage are less certain. Two main proposals have been entertained—'female choice' and 'male coercion'. Female choice was first speculated to account for polygyny in birds (Orians 1969) before equivalent ideas were adapted to human marriage systems by anthropologists (e.g. Borgehoff Mulder 1992; Josephson 1993), and the idea is very similar to the account of polygyny given by the economist Gary Becker in his landmark *Treatise on the Family* (1981). Briefly put, female choice models argue that it will be in a woman's interest to marry a married man when the cost of sharing resources with another wife is offset by his overall higher wealth, compared to marrying a relatively poorer man as his single wife. By contrast, other scholars have argued that polygyny is better understood as the consequence of male effort to control females, to the detriment of both co-wives and their children (e.g. Chisholm and Burbank 1991; Strassmann 1997). This does not necessarily imply physical coercion, but rather wider gender norms whereby women have low reproductive autonomy and a subordinate status (Smuts 1995). Like the female choice model, men of higher status are predicted to outcompete lower-status men for polygynous marriages, but in this case such a higher status is not sufficient to offset the costs of resource competition between co-wives.

In its purest form, the female choice perspective predicts that, at equilibrium, all married women should have access to the same resources, and so maternal and child health differentials between polygynous and monogamous families should be negligible. In this sense, there should be no *net* cost to marrying polygynously that would be relevant to a public health policy. Statistical adjustments for differences in wealth between families may however reveal the *hidden* costs of resource competition between co-wives. The male coercion perspective predicts that polygynously married women and their children will suffer *net* costs likely to manifest in their physical health. Table 5.2 summarizes the results of studies carried out within a specific cultural, or relatively small regional contexts that have explored relationships between polygyny and child health and/or survival. On balance, this literature appears superficially supportive of male coercion, in that children of polygynously married women are often at a significant health disadvantage and this effect is robust to at least partial controls for potentially confounding variables (see also Hadley 2005; Sellen 2009 for further discussion).

Yet, the topic remains controversial. It is attractive to conceptualise the choice and coercion hypotheses as mutually exclusive explanations for polygynous marriage, but in reality they are not so easy to distinguish and empirically evaluate as competing hypotheses, especially since wives are added to marriages sequentially and women marrying polygynously may be different to those marrying monogamously to begin with. Moreover, elements of choice and coercion will surely coexist. For example, Gibson and Mace (2007), measuring both female reproductive success and child nutritional status, report first wives in polygynous marriages in rural Ethiopia appear advantaged relative to both monogamously married women and their higher-order co-wives. Thus, being the early wife of a relatively wealthy polygynous male may be the best scenario for women, while second- and third-order wives are disadvantaged either due to costs of family resource competition or due to patterns of assortment, i.e. lower-'quality' women settling for the less desirable position of marrying an already married man (but see Strassmann 2011 for a different pattern of results by wife rank). The failure of many studies to effectively address such issues of wife rank and assortment, along with the reliance on cross-sectional rather than longitudinal studies, leaves much uncertainty about the causality in reported relationships between polygyny and health.

5.4.2 When Monogamy is Advantageous for Men

If polygyny is the preferred option for males (at least when wealthy enough to attract multiple wives), a relative absence of polygyny is logically predicted in contexts where male wealth inequality is insufficient for some men to monopolize marriage opportunities (i.e. 'environmentally imposed monogamy', Alexander et al. 1979). Indeed, there is some evidence of a positive relationship between regional wealth inequality and the incidence of polygynous marriage (Pollet and Nettle 2009). However, rates of polygyny have also been decreasing throughout sub-Saharan Africa over recent years, and in many countries, polygynous marriage is not legally sanctioned. One classic anthropological argument for why 'socially imposed monogamy' may become preferred, not only by females but also by males, is that it reduces within-group competition among men and consequently leads to benefits of greater cooperation reaped at the group level, enabling the cohesion of increasing larger societies (Alexander 1987). However, supporting evidence for such group-level benefits to monogamy has not been convincingly presented. Moreover, the logic of this hypothesis has been challenged because available data suggest that the overall variance in male reproductive success is in fact not significantly lower in monogamous societies, and that cultural norms prescribing monogamous marriage predate the establishment of large nation states (Fortunato and Archetti 2010).

Fortunato and Archetti (2010) present an alternative explanation, arguing that monogamous marriage may be better understood as a system of 'monogamous transfer' of inherited resources. They argue, supported by a formal mathematical model, that monogamy will be advantageous for men in specific contexts under two conditions: (1) provided the value of inherited resources is sharply decreased when split between the offspring of multiple co-wives and/or (2) that females strategically guarantee higher paternity to males who marry only a single wife. Thus, in specific contexts, monogamous marriage may be beneficial to both sexes; women benefit from exclusive inheritance transfers to their offspring, while men benefit from increased confidence in the paternity of their (putative) offspring. Supporting the former condition, available ethnographic and historical data suggest an association of monogamy with shifts to intensive agriculture and conditions of land scarcity, where resource transfers need to be maintained at a high threshold value to ensure the creation of viable productive and reproductive units (Fortunato and Archetti 2010). As an extension to this argument, it is also clear that preferences for polygyny should decrease with the transition to a modern cash economy as reproductive strategies shift in favour of investments in offspring 'quality' over quantity (Sect. 5.3). Evidence for the second condition, that monogamous marriage is associated with higher paternity confidence, is less clear. Indeed, there would appear to be some conflict between Fortunato and Archetti's (2010) model and the dominant view that polygyny is the product of female coercion where men are anticipated to exert dominance over women's sexuality. Interestingly, many public health studies now speculate a link between polygyny and the transmission of HIV and other sexually transmitted infections (Bove and Valeggia 2009). Hypothetically, this association could be driven by higher levels of promiscuity (and so lower paternity certainty) in polygynous societies. This conjecture however remains to be tested and relevant data on rates of paternity certainty in rural African populations, polygynous or otherwise, are scarce (but see Strassmann et al. 2012).

5.4.3 Implications for Policy

- Is polygyny best considered a risk factor for poor health? The answer to this question depends critically on its intended interpretation. On the one hand, and with respect to child health, studies carried out both at the large and small-scale have consistently demonstrated that growing up in a polygynous household is associated with relatively poor health/survival outcomes and such associations are often independent of other factors such as family size and household wealth (Table 5.2). Such information is valuable to targeted health programmes that seek to identify contexts in which children may be most in need during times of resource stress or food insecurity. It is also valuable to analysts of population health data aiming to isolate other 'risk factors' that may confound or interact with polygyny (e.g. ethnicity, maternal education, rural residence).
- However, if we take 'risk factor' to imply *causality,* there is little evidence to suggest that polygyny can be meaningfully considered a root cause of poor child health. To date, the literature, mainly relying on cross-sectional analyses, has tackled issues of causation poorly. Moreover, at the ultimate level, any apparent costs of polygyny seem best identified as a *symptom* of male coercion and low female autonomy, without which women would not enter marriages that hold negative health consequences. From a policy perspective, it is far from clear that prohibiting polygyny would reap the protective effects to women and children proposed by some scholars. In this regard, we support Gaffney-Rhys (2012, pp. 58–59), who argues that polygyny itself is not best understood as a 'harmful traditional practice' but rather as a cultural norm associated with low gender

Table 5.2 Estimated effect of polygynous relative to monogamous marriage on child health

Population[a]	Child health outcome		Notes	References
	Growth	Survival		
Dogon of Mali	–	↓		Strassmann 1997
	↓/–	↓/–	Growth: children of monogamously married women do better than children of 1st order polygynously married wives, children of 2nd, 3rd & 4th order wives are intermediate Survival: Polygyny associated with lower child survival in 8/9 villages	Strassmann 2011
Datoga of Tanzania	↓	n.a.	Growth: Children of monogamously married wives do better than children of first- and second-order polygynously married wives.	Sellen 1999
	↓/–	↓/–	Growth & Survival: Children of monogamously married wives do better than children of first-order polygynously married wives. Interactions with wealth suggested	Sellen et al. 2000
Chad (rural)	↓	n.a.		Begin et al. 1999
Yanomamö of Venezuela	↓/–	n.a.	Negative relationship in boys (tricep skinfold), no relationship in girls	Hagen et al. 2001
Rakai district of Uganda	↓/–	n.a.	Negative relationship in aggregated sample and HIV+, but not in HIV- mothers	Brahmbhatt et al. 2001
West Kiang district, Gambia	n.a.	–		Sear et al. 2002
Tonga of Zambia	↓/–	n.a.	Negative relationship to stunting for boys, but not girls	Gillett-Netting and Perry 2005
Sukuma of Tanzania	↓	n.a.		Hadley 2005
Arsi Oromo of Ethiopia	↓/–	n.a.	Child of first-order polygynously married wives not different from children of monogamously married wives, but do better than children of second- and third-order wives	Gibson and Mace 2007
Kipsigis of Kenya	n.a.	↓/-	Indication that negative effects on survival are limited to poor households	Borgerhoff Mulder 1997, 2007
Bimoba and Kusasi of Ghana	n.a.	↓		Meij et al. 2009
Banfora district, Burkina Faso	n.a.	↓		Diallo et al. 2012

[a] This table only includes studies carried out within specific communities/cultural contexts (i.e. large-scale DHS analyses not included). Studies by both evolutionary and non-evolutionary anthropologists and demographers included

Key:—no relationship, ↓ negative relationship, ↑ positive relationship, /relationship varies by subgroup (see Notes column for details); *n.a* not applicable, i.e. study did not explore this outcome equality, which is the real threat to health and wellbeing. Attention may thus be better devoted to initiatives that seek to reduce gender inequality rather than to prohibit polygynous marriage. The abolition of polygyny, without tackling the cultural position of women, could lead to unintended negative consequences. For example, one way in which polygyny may be protective to women is through the practice of the levirate, whereby a widow joins the marriage of her deceased husband's brother, without which older widowed women may have difficulty accessing resources required to maintain their own health and welfare.

- We also caution that polygyny may become associated with disadvantage because of culturally insensitive health programmes that neglect its very existence. For example, Bove and Valeggia (2009) consider an initiative in Botswana, where men with HIV+ serostatus were offered free antiretroviral treatment in addition to medication for *one spouse only*. In this case, a well-intentioned policy may actually *create* relative disadvantage in polygynous households simply because they fail to fit the Western norms of monogamous marriage.
- Lastly, we note several reasons why analyses of large-scale nationally representative DHS surveys should *not* be prioritised for policymakers interested in the effects of culturally related variables such as marriage practice. Firstly, there are often important ethnic-related differences in health within countries, and regional boundaries (e.g. Brockerhoff and Hewitt 1998). However, DHS studies have typically neglected to adjust estimates for ethnicity, which will most likely confound with marriage systems (e.g. Amey 2002; Gyimah 2009; Omariba and Boyle 2007). Secondly, anthropological studies have more often been able to utilize longitudinal data and information on wife rank (e.g. Gibson and Mace 2007; Strassmann 2011). The DHS on the other hand are cross-sectional and data on wife rank are generally absent or of poor quality (Omariba and Boyle 2007). Finally, there are important issues with respect to categorization and statistical treatment of polygynous households in the DHS, which are poorly designed to deal with non-nuclear families (Randall et al. 2011). For example, it is unclear how to interpret adjustments for household wealth when men only reside with one wife, while additional wives live in apparently separate but often adjacent and economically co-dependent households.

5.5 The Role of Extended Kin

In both the social and health sciences, most research on family structure is situated in the developed world, particularly Western Europe and North America, seriously biasing the current knowledge base available to population scientists and policymakers alike (Adams 2004; Gyimah 2009; Penn 2012). In these countries, the 'nuclear family' is both the norm and the socially recognized ideal—with wife, husband, and children living in relative isolation and economic independence from other kin. However, in the developing world, nuclear family living is in fact rather rare (Lloyd and Desai 1992; Sear 2011). As we have already discussed, polygynous marriage is not uncommon. There is also great cross-cultural variation in the role of fathers. Some 'partible paternity' cultures in South America even identify multiple fathers for single offspring based on the mother's sexual relationships during or close to pregnancy (Walker et al. 2010). Moreover, married couples, particularly in rural environments, typically live with, or very close to, the wife's or husband's extended family, and resources are generally shared across wider networks. Some cultures tend towards matrilocality (females stay in or near their natal home, and men move at marriage, although often not very far), while patrilocality is generally more common (males stay and females move), especially since the advent of agriculture (Wilkins and Marlowe 2006).

In many parts of the world, rates of fosterage and orphanhood are also high and, due to the HIV/AIDS epidemic, have grown substantially in recent decades. Thus, in sub-Saharan Africa, it has been estimated that one in ten children under the age of 15 have lost at least one parent, while one in six households care for a child with a dead mother or father (Roeland and Ties 2004). In cases where children have lost both parents, they are almost always found in the care of the extended family (Roeland and Ties 2004). How best to deal with rising orphanhood has become a key area of policy relevance, with some arguing that traditional kin-based systems of orphan care have been stretched to breaking point by the impact of the epidemic, and others suggesting the extended family, particularly if supported by appropriate interventions, can still support a large number of orphans (for a discussion, see Abebe and Aase 2007; Mathambo and Gibbs 2009). In addition to the issue of substitute parents, understanding the importance and differing priorities of extended kin is also of broader relevance to population health. This is because as senior family members, both in and outside the presence of biological parents, extended kin are expected to influence patterns of household production and consumption, including patterns of health expenditure (Dupas 2011).

Although rarely directly engaged with the debates above, evolutionary anthropologists have now accumulated a large body of relevant literature on the role of extended kin (Bentley and Mace 2012; Coall and Hertwig 2010; Hrdy 2009; Sear and Mace 2008). Interest in this area is motivated by theories of kin selection, since childcare is an altruistic act predicted to vary in response to genetic relatedness (Box 5.1c). Studies have also sought to elucidate the factors responsible for the unusual features of human life history. In particular, assistance from extended kin is argued to have enabled humans to simultaneously maintain a high reproductive rate and extended juvenile dependency compared to other primates of a similar body size (Hawkes 2003), leading some to categorize humans as 'cooperative breeders' (Hrdy 2009; Sear and Mace 2008; but see Strassmann 2011). Furthermore, the influential 'grandmother hypothesis' argues that grandmaternal support accounts for why humans are unique among primates in experiencing menopause, i.e. the irreversible cessation of reproductive potential at around 50 years of age. Throughout human evolution, women above this age are proposed to have been better able to enhance their inclusive fitness by assisting existing offspring to care for children than they would by having additional children of their own, due to increased difficulties in childbirth and a reduced chance of surviving long enough to ensure adequate postnatal care (Hawkes 2003; Shanley et al. 2007; Williams 1957).

5.5.1 Mothers and Others

Sear and Mace (2008) recently collated data from a large number (n=45) of anthropological and demographic studies considering how the presence/absence of alternative categories of kin (usually measured as currently alive or dead) influences child survival in contexts of high child mortality and high fertility. This review provides a useful survey of the relative importance of different family members. Unsurprisingly, children whose mother died before they reached their second birthday had dramatically reduced likelihood of survival, demonstrating that infants are almost exclusively reliant on maternal care. Yet, for children whose mother died after this age, the likelihood of survival was often remarkably high, suggesting that for weaned children maternal care is frequently replaceable, at least with respect to survival outcomes. In most studies, the absence of a father made no difference, and was associated with reduced survival in only one-third of studies with appropriate data. However, in line with expectations from the grandmother hypothesis, around two-thirds of studies reported that the grandmother's presence was associated with improved child survival. Maternal grandmothers were more important than paternal grandmothers, and, in some cases, the presence of paternal grandmothers was negatively rather than positively related to child survival (see also Strassmann and Garrard 2011). With regard to other categories of kin, the presence of grandfathers was generally inconsequential, and, in the few studies with relevant data, the presence of elder siblings was often positively associated with survival confirming that older children can often play an important role as alloparents (see also Kramer 2005). The presence of aunts and uncles was also occasionally correlated with higher child survival, but few studies contained relevant data. Sear and Mace (2008) conclude that help from kin is a ubiquitous feature of human societies, but which kin matter in keeping children alive is highly variable between populations.

The literature reviewed by Sear and Mace (2008) concerns mainly farming and patrilocal populations. This bias however fits the reality of the majority of contemporary rural developing populations. More seriously, correlation in the survival/presence of kin and child survival does not confirm causality. A focus on survival may also obscure more subtle inequalities in health and wellbeing. Some studies have been able to demonstrate the importance of grandmothers more directly. Gibson and Mace (2005), for example, found that the presence of maternal grandmothers in particular was associated with improved child growth and report time allocation data indicating that grandmothers were important in relieving daughters of domestic chores (see also Hawkes et al. 1997). Strassmann (2011), however, cautions that extended kin may not always be beneficial, and that coresident elderly grandparents may be more likely to be net consumers in resource-poor settings. In her long-term study of a Dogon agriculturalist population in Mali, child growth and survival were not improved in the presence of extended kin, and child mortality increased in the presence of paternal grandmothers. Recent studies also emphasize that the benefits of paternal involvement may be underestimated by focusing on early life health outcomes alone. Scelza (2010), for example, reports that in Australian Martu Aborigines, the presence of fathers accelerates the timing of ritual initiations and consequently later social and reproductive success.

5.5.2 Relatedness and Extended Family Care

Why do maternal grandmothers more consistently improve child health than paternal grandmothers (Sear and Mace 2008; Strassmann and Garrard 2011)? Kin selection theory presents a strong candidate explanation. When paternity is uncertain, the inclusive fitness benefits of investment will be on average higher for maternal grandparents than paternal grandparents. Although the required genetic data are difficult to come by, there is evidence that paternity is indeed often uncertain to a non-trivial degree in humans (Anderson 2006), supporting the view that paternal relatives are less likely to be genetically related to their putative grandoffspring. There is also evidence that fathers are aware of cues of physical resemblance and alter investment accordingly (e.g. Alvergne et al. 2009b). Furthermore, a number of studies have confirmed similar biases in the investment of maternal and paternal grandparents, as well as aunts and uncles, in more modern populations (Coall and Hertwig 2010; Gaulin et al. 1997).

Alternative, and not necessarily mutually exclusive, explanations have also been presented for the asymmetry between paternal and maternal grandmother effects. Strassmann and Garrard (2011) stress the role of local resource competition, arguing that in patrilocal populations grandparental presence may often be less beneficial or even detrimental to children because they are both consumers of the same pool of family resources. It is also true that in populations where men typically marry and reproduce at a later age, paternal grandparents will be older and so may be simply less likely to be healthy enough to provide support (Strassmann and Garrard 2011). Distinguishing between these hypotheses is difficult on the basis of studies of kin presence and child outcomes alone. More direct data on the care roles and consumption/production activities are therefore required. See also Coall and Hertwig (2010) for a thorough review of the other factors predicted to account for variation in grandparental care, from both evolutionary and non-evolutionary theoretical frameworks.

Recently, it has been argued that investment of paternal and maternal grandmothers will also interact with child sex due to differing relatedness on the X-chromosome, which is estimated to contain approximately 8 % of all human genes (Fox et al. 2010). Assuming no paternity uncertainty, X-chromosome relatedness between paternal grandmothers and female grandchildren will be 50 %, because fathers transmit the only X chromosome they receive to their daughters, whereas it will be 0 % for male children, since they receive a Y rather than an X chromosome. From maternal grandmothers, X-chromosome relatedness to both male and female grandchildren children is 25 %, since any given X-linked gene has a 50 % chance of being passed from grandmother to mother, and again from a mother to either her male or female offspring. Analysing data from seven traditional populations, Fox et al. (2010) found in all populations that boys were more likely to survive in the presence of maternal grandmothers rather than paternal grandmothers, in 4/7 populations girls were more likely to survive in the presence of paternal grandmothers rather than maternal grandmothers, and in 6/7 populations paternal grandmothers had a more positive influence on female than male survival. The mechanisms behind these findings remain to be investigated, but these initial findings appear supportive of Fox et al.'s predictions. It is also hard to imagine how a non-evolutionary framework could predict such a pattern of results.

5.5.3 Implications for Policy

- The most obvious contribution from the anthropological literature on the extended family is that there is nothing 'natural' or intrinsically advantageous about the nuclear family set-up (Bentley and Mace 2012; Hrdy 2009). Yet, as Penn (2012) argues, global health recommendations regarding how children should be raised draw heavily on long traditions of child development research situated in modern Western societies (e.g. WHO 2004). Findings of evolutionary anthropologists therefore deserve to be disseminated widely to an applied audience, contributing to a new synthesis of how best children can be cared for in the developing world where child-rearing environments are often dramatically different.
- What, if anything, can evolutionary anthropology say about the ability of extended kin to absorb the increasing number of AIDS orphans in sub-Saharan Africa? The literature above certainly confirms that extended kin often play an important role in rearing children, father presence is often not related to child mortality, and that even maternal death is often an at least partially recoverable tragedy. However, it also suggests that when conditions are poor, children and extended kin are more likely to be competing for resources (Strassmann 2011; Borgerhoff Mulder 2007). Thus, it is likely that traditional kinship-based care systems can only be considered a meaningful resource for orphans provided a family has not fallen below a certain poverty threshold. Future research should prioritise exploring this interpretation and identifying how such a threshold can be best defined in a way useful for policy design.
- Recent population health literature has rejected a unitary model of household interests, with the effectiveness of health interventions differing depending on which family member is targeted. For example, a number of studies have shown that grandmothers and mothers spend more income improving child health and development than grandfathers and fathers (Dupas 2011). Evolutionary anthropology has much unmet potential as a predictive and interpretive tool with regard to studies of this kind. It also suggests future studies should consider not just differences by sex, but also relatedness. Duflo (2003), for example, finds that the receipt of pension by grandmothers in South Africa improved the health of granddaughters, but had relatively little effect on grandsons. Assuming that most coresident grandmothers are likely to be paternal in this population, this result is intriguingly consistent with the predictions of Fox et al. (2010), i.e. that paternal grandmothers will favour female grandchildren.

5.6 Conclusions

In this chapter, we introduced the evolutionary anthropological perspective on the human family and reviewed its predicted and observed relationship to physical health in the developing world. Where appropriate, we have drawn tentative implications for population policy. What can evolutionary anthropology contribute to population health science? We hope we have been successful at demonstrating at least two major contributions. Firstly, we believe evolutionary anthropology usefully contributes an integrative 'top-down' theoretical framework linking thinking about the *causes* of variation in family structure across space and time with current debates on the *consequences* of alternative family structures on physical health and related measures of wellbeing. Secondly, evolutionary anthropologists have amassed a considerable body of quantitatively sophisticated literature on the complex bidirectional relationships between family structure and health. The results of these studies are of raw empirical value regardless of whether or not one subscribes to an evolutionary perspective. Anthropological studies are particularly valuable given their traditional focus on community samples within well-described cultural contexts, complementing the contrasting reliance on large-scale secondary demographic data sets in population health science (David and Haberlen 2005).

The literature reviewed here is also notable in its strong emphasis on context dependency. Indeed, evolutionary anthropologists explicitly argue that the great diversity of human social organization ultimately springs from the very fact that the pay-offs to alternative ways of living are highly contingent on individual and socioecological circumstance (see also Kaplan et al. 2009). This emphasis reinforces traditional anthropological concerns over the inherent dangers of ethnocentrism, i.e. the tendency to judge other cultures by the values and standards of one's own culture. Furthermore, from a policy perspective, it encourages a healthy scepticism with regard to 'blanket' initiatives which implicitly assume equal incentives for behaviour change will apply across a wide range of environments (e.g. nationwide policies spanning both urban and rural contexts). From a more methodological standpoint, the anticipation of high levels of context dependency also presents a strong a priori argument for valuing improved collection and analysis of contextual data at both the family and population level (see also Bock 1999). Large-sample DHS analyses of family structure and health, for example, do not typically include detailed information on the nature of rural livelihoods, often neglect ethnic variation that may confound with variables under study, and rarely sample a sufficient number of households within specific communities that would be required to identify context dependency at the local level. Evolutionary anthropologists, building on a deeper tradition in anthropological demography (e.g. Kertzer and Fricke 1997; Randall et al. 2011), thus have an important role to play in highlighting the limitations of prioritising representativeness and inclusivity at the sacrifice of potentially more meaningful context-specific analyses of population dynamics and health.

Greater exchange with evolutionary anthropology may also provide population health scientists with new knowledge on the existing strategies that disadvantaged peoples in the developing world already use to mitigate risk and uncertainty in the absence of external intervention. We note, however, that adaptive strategies will be those that prioritise inclusive fitness not personal wellbeing (Hill 1993), and the interests of the individual over the interests of one's partner, children, or wider group. Human behaviour, in any population, may therefore rarely be optimal with respect to maximizing health and minimizing inequality. In any case, a commitment to understanding human adaptation may help us understand why specific initiatives succeed or fail. For example, Hampshire et al. (2009) reflect on the conflict between humanitarian efforts to save the lives of the most-needy children in the context of a severe food crisis in Niger and the efforts of local people to prioritise the preservation of livelihoods and long-term household sustainability. While not taking an explicitly evolutionary perspective, they argue that the efficiency of emergency nutrition programmes, such as the distribution of food supplements to needy households, could be improved by recognizing that parents lack incentives to prioritise the sickest children when overall household survival is maximized by allocating food more equally, or to those most able to engage in the generation of household resources. See also Rende Taylor (2005) for a similar case study regarding parental motivations for child labour in Thailand.

Perhaps the most contentious issue with evolutionary anthropology, both within and outside the discipline, is the extent of maladaptation in human behaviour, particularly in circumstances of environmental novelty (Brown et al. 2011; Nettle et al. 2013). This issue is particularly pertinent to those developing populations undergoing rapid socioeconomic development, where we can expect both genetic and cultural lag to disrupt adaptive responses. Indeed, the universal fertility decline associated with the transition to a developed economy appears to be best understood as a maladaptive product of exceptionally strong trade-offs between fertility and economic investments in self and offspring (Goodman et al. 2012; Kaplan 1996). In this case, adaptive lag is clearly beneficial to population health, even if detrimental in terms of genetic fitness. In other cases, mismatch may be more likely to threaten wellbeing, perhaps particularly for those individuals experiencing rapid social or ecological change within their own lifetime so that the futures they have prepared for fail to materialize (Stevenson and Worthman 2013).

We concede that to an important extent adaptive lag, by removing the assumption that individuals will conform to adaptive expectations, clouds the predictive value of evolutionary anthropology. There is also much debate within the field regarding how much our unique capacity for cultural transmission should lead us away from the conventional framework of optimality modelling (Borgerhoff Mulder 2013). However, the fact that evolutionary anthropology is still working out how best to 'deal with culture' can hardly be seen as a tangible criticism in comparison to population health science, where culture is commonly presented as an explanation for health outcomes and disparities, but rarely defined, measured, nor directly evaluated as a plausible determinant (Hruschka 2009). The primary strength of the evolutionary anthropology paradigm is thus not its marriage to a particular set of assumptions, but rather that it combines a strong commitment to ask the complicated questions about *why people do what they do* with an equal commitment to evaluate alternative hypotheses with the available data. Not doing so is to rely blindly on rhetoric and implicit assumptions about human nature. We hope this chapter will go some way in drawing an additional audience to the evolutionary anthropological literature and that further exchange with population health scientists will continue to yield both academic and applied insights on the human family.

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Chapter 6
Declining Breastfeeding Rates Among Immigrant Populations: A Look Through an Evolutionary Lens

Alejandra Núñez-de la Mora

Abstract In the UK, immigrant women from developing countries are more likely to initiate breastfeeding and sustain it for longer periods than women in the nonimmigrant white population. This desirable pattern, however, is being eroded among UK-born generations where incidence and duration of lactation are significantly lower than in first-generation immigrants. I use concepts and principles derived from life history theory and human reproductive ecology to explore how the physical environment may affect the costs and benefits of alternative breastfeeding strategies. Specifically, I compare two ecological scenarios: one of high infectious risk and energetic constraint like the one prevailing in the countries of origin of many immigrant communities versus one of low infectious disease risk and energy surplus characteristic of host countries like the UK. I contrast the results with the empirical findings on breastfeeding rates obtained during a migrant study conducted among first- and second-generation Bangladeshi women living in London. Finally, I discuss how the insights obtained taking an evolutionary approach may be incorporated into programmes and policies related to infant feeding practices and maternal health among immigrant populations.

6.1 Introduction

In the UK, ethnic minority women are more likely to initiate breastfeeding and sustain it for longer periods than women in the white population (Griffiths and Tate 2007; Griffiths et al. 2005; Kelly et al. 2006). It appears, however, that this desirable pattern is being eroded among younger generations of women in these groups: The incidence and duration of lactation are significantly lower in UK-born women than in first-generation immigrants (Hawkins et al. 2008). The deterioration in maternal health behaviours, including declining breastfeeding rates, has been documented in other countries with large immigrant populations (Bonuck et al. 2005; Celi et al.

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2005; Gibson-Davis and Brooks-Gunn 2006; Rassin et al. 1993). The detrimental change in feeding patterns among immigrants is cause for great concern for public health specialists, health authorities and policymakers alike as it can exacerbate and perpetuate health and social inequalities already prevalent among many ethnic minority groups (Nazroo 2003).

The majority of studies addressing the issue of changes in health behaviours among immigrant populations has focused on structural aspects (i.e. changes in socioeconomic conditions (Chen 2009; Singh et al. 2007) and the related effects of acculturation (Hawkins et al. 2008)). For breastfeeding behaviour, in particular, researchers have described associations between variables such as language proficiency, composition of social circles and length of residence as proxies for degree of assimilation (Choudhry and Wallace 2012; Gibson et al. 2005; Rassin et al. 1993).

Research on the causes behind the modification of infant feeding practices upon migration in the UK is scarce and is biased towards the South Asian community, the largest in immigrant population size (ONS 2012). Motivated by a pragmatic need to improve health promotion, access and health-care provision, studies have concentrated on identifying attitudes, expectations and perceived barriers to successful breastfeeding and the specific needs for support in the domestic, public and institutional spheres of women of different ages, generations and degree of acculturation (Choudhry and Wallace 2012; Ingram et al. 2008; Twamley et al. 2011; Women's Health and Family Services 2007; Woollett et al. 1995).

In contrast, research aimed at unpacking the complexities of changing ecologies upon migration and their effect on breastfeeding trends has, to my knowledge, received practically no attention. In this chapter, I use concepts and principles derived from life history theory and human reproductive ecology to explore how the physical environment may affect the costs and benefits of alternative breastfeeding strategies. I apply these ideas to the issue of declining breastfeeding rates among younger generations of immigrants in the UK and argue in favour of the potential of ecological models in informing interventions on issues of maternal and infant health.

6.2 Lactation as Plastic Parental Investment

Some of the traits that characterise humans as a species and that appear to have been key to its success make human babies very expensive to produce (Wells and Stock 2007). Human babies are born fatter, larger and heavier relative to maternal size than our closest primate relatives (Kuzawa 1998); they are born utterly dependent (altricial), and require considerable care over a protracted childhood of slow growth until they can fend for themselves (Dufour and Sauther 2002; Mace 2000). As in other mammals, human females bear the bulk of the reproductive burden, in terms of energy, time and opportunity costs, especially during gestation and lactation.

Lactation is a key component of early parental care and the major primary mechanism among mammals for provisioning dependent offspring during the first years of life (Prentice and Prentice 1988). Aside from providing complete nutrition, breastfeeding protects infants against gastroenteritis, respiratory infection and various other illnesses (Chien and Howie 2001; Howie et al. 1990; Quigley et al. 2007). Breastfeeding has also been shown to have positive long-term consequences for metabolism, cognitive and psychomotor development and disease risk later in life (Hornell et al. 2013; Oddy et al. 2012; Sacker et al. 2006). Many of the benefits of breast milk are dose responsive (Raisler et al. 1999) and persist beyond termination of breastfeeding (Oddy 2001). Thus, beyond its mid-term effects on survival (WHO Collaborative Study Team on the Role of Breastfeeding on the Prevention of Infant Mortality 2000), lactation could also have fitness consequences for the offspring through enhancing traits related to reproductive success.

The energetic costs of human lactation are a consequence of milk synthesis and the maintenance of metabolically active mammary glands (Butte et al. 2001; Prentice and Prentice 1988). Although fairly efficient, the daily extra cost is nearly double that of pregnancy, and represents as much as 50% of a woman's total energy budget in undernourished populations (Vallegia and Ellison 2001). Mothers may meet the energy debt by increasing food consumption, reducing physical activity and/or lowering their basal metabolic rate (Dufour and Sauther 2002); however, in energy-restricted populations, women are forced to metabolize their stored fat reserves to cover the balance (Adair and Popkin 1992). In circumstances of extreme energetic constraints, recurrent cycles of closely spaced pregnancies and prolonged lactation may result in 'maternal depletion syndrome' with negative implications for the mother's and offspring's health (Dewey and Cohen 2007; Merchant et al. 1990; Winkvist et al. 1992). In addition to the direct impact of lactation on maternal nutritional status, the energetic and time demands of breastfeeding may have an indirect effect by restricting maternal activities related to food production (Panter-Brick 1991) and care provision to other existing offspring and kin (Quinlan et al. 2003).

In terms of opportunity costs, lactation impacts a woman's reproductive capacity by prolonging the period of postpartum amenorrhoea during which ovarian function is suppressed and chances of conception are low (Rogers 1997). The resumption of functional ovarian cycles is very variable and it is largely determined by how lactating practices interact with maternal energetic status (Ellison and Valeggia 2003; Valeggia and Ellison 2009). Across different populations, regardless of subsistence patterns, women who breastfeed resume menstruation later than women who do not. In natural populations, the former experience longer intervals between births and an overall slower reproductive rate than the latter.

For most of their evolutionary history, human females have reproduced under conditions typically marked by energetic constraints. Apart from the variable food availability, heavy physical loads and high morbidity associated with adverse environments, modern human females would have experienced highly seasonal ecologies, where energy was not only limited but also inconsistent (Wells 2012). Under such selective pressures, humans are expected to have evolved the ability to monitor the environment and integrate ecological and social information in order to optimise the trade-offs between the costs and benefits of lactation so as to maximise reproductive fitness. For humans, the plasticity of lactation patterns in the face of environmental change would have great adaptive value.

6.3 A Life History Model for Breastfeeding Strategies in Two Contrasting Ecological Settings

In this section, I assess the behavioural responses to two specific scenarios, each defined by ecological characteristics that constitute strong selective agents: overall energy availability and pathogen exposure (Wells 2012). The aim is to compare the consequences of lactating in two contrasting environments in terms of offspring survival, maternal energetic status and fertility (all components of fitness), and to discern, on the basis of the implied trade-offs, the lactation strategy that would be expected in each case.

At the core of this discussion is the notion that lactation, like any form of depreciable parental investment, is expected to result in maternal trade-off decisions about its allocation. The expectation is that, by modifying the different structural components of breastfeeding, women are able to calibrate their investment in the component of fitness that is likely to accrue them the highest returns given the circumstances: either through favouring investment in the current offspring by enhancing its chances of survival or through increasing her potential to invest in a new one. In other words, alternative lactation strategies allow women to place their bet either on their current or their future reproduction according to cues obtained from their environment.

Breastfeeding is, by definition, an interaction between two individuals for whom the costs and benefits may not always be aligned. Here, the analysis of each breastfeeding strategy and its resulting trade-offs are considered in relation to the mother's perspective, in particular in how these affect her reproductive success; the interests of the infant are discussed to the extent that they affect the mother and the outcome of her strategic decisions.

The aim here is to offer an illustration of how an evolutionary approach can contribute fresh insights into the issue of behavioural change. This exercise focuses only on overall duration of breastfeeding. I do not consider variation in any other component of breastfeeding such as intensity, frequency and type of feeding (either exclusive or mixed), all of which have a direct impact on the energetics of lactation and can indirectly affect the resumption of fertility (Chao 1987).

Finally, since the focus of this discussion is to compare two alternative lactation strategies rather than to calculate an optimal duration of lactation for each local scenario, duration of breastfeeding has been categorised somewhat arbitrarily as 'short' and 'long'. Based on the cross-cultural evidence that suggests the biologically determined lower bound for safe supplementation is around 6 months of age (Sellen 2007), 'short duration of breastfeeding' is taken here to be of at least 6 months. In-

Table 6.1 Description of the variables relevant to fitness in each of the two ecological scenarios

Variable	*Scenario 1*: Bangladesh	*Scenario 2*: UK
Pathogen risk	High	Low
Energy availability	Low	High
Infants		
Risk of infection	High	Low
Risk of undernutrition	High	Low
Survival penalty of closely spaced births (short inter-birth intervals)	High	Low
Mothers		
Costs of basal maintenance	High	Low
Risk of maternal depletion	High	Low
Baseline levels of ovarian function	Low	High
Probability of conception during lactation	Low	High
Duration of postpartum amenorrhoea	Long	Short

cidentally, this lower bound coincides with the current World Health Organization (WHO) recommendation (WHO 2002) and appears to be determined by constraints on the growth and maturation of infant systems affecting immune, feeding and digestive competency (Sellen 2009). Correspondingly, 'long duration of breastfeeding' here is considered any duration longer than 6 months. The characteristics of each scenario with respect to the variables relevant for both the mother and infant's fitness that are considered in the comparison are shown in Table 6.1.

6.3.1 Pathogen Risk, Energy Availability and Infant Vulnerability

Infant survival is, at its most basic, largely determined by nutritional status and pathogen exposure. Infectious disease is one of the main causes of morbidity in children under 5 years of age in developing countries where it also constitutes a crucial component of infant and childhood mortality risk (WHO 2005). In this background of threat to early survival, breastfeeding provides the bulwark of defences against infection risk. This protective effect is illustrated by the findings of a WHO-conducted analysis in 14 different countries where it was calculated that failure to breastfeed during the first months of an infant's life increases the risk of diarrhoea by a factor of nearly five and raises the risk of mortality from diarrhoea by a factor of 15, regardless of levels of hygiene and socioeconomic status (Feachem and Koblinsky 1984). The benefits of breastfeeding are also evident in findings that show that infants who continue breastfeeding for at least 4 months or more have a significantly reduced risk of respiratory infection both in developing (Kramer and Kakuma 2012) and developed countries (Ip et al. 2007). Moreover, given the independent and synergistic, deleterious effects that poor nutrition and disease have on infant growth and survival (Pelletier 1994; Rodriguez et al. 2011; Scrimshaw 1975), the nutritional and immune benefits of breastfeeding may be particularly decisive for infants born in vulnerable ecological conditions, where prolonged lactation would give the highest returns.

6.3.2 Energy Availability, Maternal Status, Reproductive Function and the Reproductive Costs of Lactation

Well-nourished breastfeeding women can maintain high milk output even through the second year of lactation (Butte et al. 2001). However, despite a series of physiological and behavioural, energy-sparing mechanisms to buffer lactation (Dufour and Sauther 2002), the relative costs of lactation can be onerous for women living in poor ecologies, and can lead to deterioration of nutritional status and even maternal depletion syndrome where the ability to recoup expended nutritional reserves is limited (Adair and Popkin 1992; Merchant et al. 1990). Maternal depletion not only jeopardizes maternal health and the wellbeing and survival of existing offspring (Widen et al. 2013) but also significantly diminishes a woman's potential for future reproduction.

The relationship between fertility and overall energy availability is mediated through the effect of maternal energetic status on ovarian function (Ellison et al. 1993b) and, in turn, on the probability of conception in any given cycle (Lipson and Ellison 1996). Women living in conditions of chronic energetic constraints show baseline levels of ovarian steroids and ovulation rates that are significantly lower than women in less restrictive environments (Ellison et al. 1993a; Vitzthum et al. 2002). Thus, at baseline, energetically stressed women have a comparatively lower chance of conception than their affluent counterparts. Such associations between ovarian function and energy availability are expected to be compounded by the energetic demands of lactation. Given the determinant role of maternal energetic status in the duration of amenorrhoea and the resumption of postpartum fecundity (Ellison and Valeggia 2003; Valeggia and Ellison 2009), energetically stressed women are expected to experience a longer period of lactational amenorrhoea and a longer phase of dampened ovarian function once menses resumes compared to women in better energetic condition (Rogers 1997).

In terms of fertility then, women in deprived environments would have longer waiting times to the next birth and slower reproductive rates than women in affluent environments, making the lactation costs associated with reproductive potential relatively higher for the former. Such losses, however, may be partially offset by the increasing probability of offspring survival that the resulting long inter-birth interval confers (Alam 1995; Palloni and Millman 1986).

A critical thing to consider when assessing opportunity costs of lactation in relation to current versus future reproductive investment relates to the factors that impact the actual probability that the woman will be alive to reproduce in the future (Stearns 1992). Apart from the obvious effect of maternal age, external environmental factors associated with high mortality risk have the potential to tilt the balance towards investment in current reproduction. In this sense, women in ecologies where

Table 6.2 Infant survival and reproductive trade-offs of long and short lactation strategies for each local ecological scenario

Lactation strategy	Relative benefits on infant survival	Relative benefits in reproductive opportunities
Scenario 1. High pathogen risk/low energy availability—Bangladesh		
Short breastfeeding	+ or − if less than 6 months	+
Long breastfeeding	+++	−
Scenario 2. Low pathogen risk/high energy availability—UK		
Short breastfeeding	+	+++
Long breastfeeding	+ but devalued with time	+

the combination of morbidity and negative energy balance are likely to reduce maternal lifespan may be more likely to favour their current offspring's survival over the uncertain prospect of a future one. The differential effect of environmental energy availability and the associated relative costs of lactation in terms of reproductive potential described above are summarised in Table 6.2.

Overall, this model suggests that for women living in ecologies where the energetic constraints normally associated with nutritional and pathogen risks are low, prolonged lactation results in comparatively lower dividends in offspring survival terms and yet potentially higher relative reproductive costs than if infants are weaned earlier. In contrast, for women in poorer settings, where infant vulnerability is high and reproductive opportunities are reduced by a comparatively less robust reproductive function, the fitness benefits of ensuring offspring survival through prolonged lactation outweigh the costs of relatively improbable reproductive opportunities.

6.3.3 Limitations of the Model

Although helpful to generate testable hypotheses based on evolutionary principles, the model presented here is limited in a number of ways. First, a lactation strategy defined in terms of overall breastfeeding duration provides an imperfect and incomplete picture of the patterns that are likely to occur in the real world. Lactation is a continuous process and, more often than not, involves the introduction of complementary foods at different ages, in different amounts and for various lengths of time before the actual termination of breastfeeding occurs. The implication of such variability, in terms of energetic costs for the mother and of benefits for the infant, may be significant and therefore affect the trade-offs on which decisions are made. In consequence, two women with equally long periods of lactation but rather different timing and degree of supplementation may face quite different trade-offs.

Another related issue is that the model is an intentional oversimplification to highlight the proximate ecological variables affecting the duration of breastfeeding in relation to pathogen risk and the consequences for infant survival. However, the reality involves a much more complex array of biosocial and cultural elements that impact and modulate maternal decisions about the patterns of lactation adopted (see McDade and Worthman 1998). These reservations notwithstanding, I believe this evolutionary-based model provides a novel or innovative platform for interpreting empirical data on breastfeeding patterns in diverse populations, including the UK-Bangladeshi community in the study described below.

6.4 The Bangladeshi Migrant Study

Since the pioneering work by Boas, a century ago, migrants studies have been used as natural experimental models to assess the impact of specific as well as changing environments (biological and social) on human plasticity (Lasker 1995; Lasker and Mascie-Taylor 1988). The comparison of immigrants versus sedentees (non-migrants) has helped our understanding of how phenotypic, developmental and behavioural patterns change after migration, as well as to identify factors in the new environment responsible for those changes. This approach has been invaluable in shedding light on the effects of biocultural practices on disease risk, as well as in describing intergenerational trends in health outcomes (e.g. Gagnon et al. 2009; Nelson 2006; Patel et al. 2012). In this section, I describe a migrant study originally designed to compare hormonal profiles and reproductive patterns among subsequent generations of adult immigrant women who, by moving from Bangladesh to the UK, had experienced contrasting environmental conditions during different phases of their life cycle (Núñez-de la Mora et al. 2007). As part of the protocol, detailed data on breastfeeding behaviour were collected.

Below, I give a brief profile of the study population and outline some general aspects of the ecologies in the countries of origin and destination. I present a summary of the differences in breastfeeding patterns found among first- and second-generation women and discuss the findings in light of the evolutionary model described in the previous section.

6.4.1 Study Population and Pre- and Post-Migration Environments

Bangladeshi immigrants in London were selected as a study population because they originate from a country whose economic, developmental and health indicators are strikingly different from those of the UK (UNICEF 2013; WHO 2013), allowing for a clear contrast between pre- and post-migration environments. For instance, in Bangladesh which is one of the poorest nations in the world, the gross national product (GNP) is only 1.4 % that of the UK, the prevalence of low birth weight is

Fig. 6.1 Ancestral homes, 'baris', in Sylhet District, Bangladesh, in the dry season

quadruple that of the UK, the average life expectancy for women is 13 years shorter and the infant mortality rate is nine times higher than in the UK (World Bank 2013).

Most Bangladeshi immigrants in the UK originate from Sylhet District in the northeast of the country (Gardner 1995). They share similar migration and socio-economic histories (Carey and Shukor 1985; Eade et al. 1996), constitute a multi-generational population (Champion 1996; Haskey 1997) and rarely intermarry with other ethnic groups (Berrington 1996). A large proportion belongs to relatively affluent, land-owning classes who live in solid dwellings and do not typically experience food insecurity (Gardner 1995). Nevertheless, their ancestral homesteads or 'bari' generally lack appropriate sewage and waste disposal systems, have limited water treatment capacity and experience seasonal flooding (Bangladeshi Bureau of Statistics 2009, 2011; Fig. 6.1). Such unsanitary conditions are largely related to the high protozoan parasitic infections and diarrhoeal disease prevalent in the whole of Bangladesh (Boschi-Pinto et al. 2008; Ward 2009). This insalubrious situation is further compounded by the limited and inadequate health-care provision available (Hoque et al. 2012; Murphy et al. 2013). The notion that such adverse environmental conditions render even middle sectors of the Bangladeshi society vulnerable to disease was corroborated by reports from participants in the migrant study who confided several cases of infant-related childhood deaths among their close circle of relatives and friends.

In the UK, Bangladeshis are one of the most socially and economically disadvantaged of all ethnic groups (ONS 2012). Nevertheless, the overall quality of the environment, including free access to good health services and a clean water sup-

Fig. 6.2 **a** Street scene in Sylhet town, Bangladesh. **b** Street scene in East London, UK

ply, represents a stark contrast to the conditions in their home country (Fig. 6.2). If nothing else, immigrants to the UK are no longer chronically exposed to infections, an improvement that should translate into enhanced growth and maturation (Cole 2000).

Cross-sectional studies show that better growth parameters are indeed achieved by immigrants upon arrival in the UK. For example, published figures for growth trajectories of infants and children of South Asian background are comparable to 1990 UK growth standards (Kelly et al. 1997). Similarly, statistics recorded in successive immigrant generations show evidence for a secular trend towards increased height, especially in females (Shams and Williams 1997). Further health indicators related to infant mortality and childhood morbidity support the idea of improved environmental conditions in the UK for Bangladeshi immigrants. For instance, the postneonatal mortality rate between 1987 and 1990 for infants born to Bangladeshi mothers living in East London (where the majority of immigrants live) was 6.9 per 1,000 live births (Hilder 1994), one-seventh as high as the national rates of 97/1,000 births for Bangladesh for that period (World Bank 2013). This contrast is significant even against the infant mortality rates reported for the richest sectors (58/1,000) and highest level of education (49/1,000) quintiles in urban Bangladesh (Bangladeshi Bureau of Statistics 2011).

Moreover, data show that the highest rates for childhood tuberculosis among children of Asian ethnicity are recorded for children born outside Britain. Similarly, the prevalence of hepatitis B among South Asian pregnant women is higher in those born abroad compared to that in the general British population (ONS 2004). In addition, a study among Asian women attending an antenatal clinic in England found that 45 % of the Bangladeshis were infected with at least one of three species of worms, while the prevalence of infection decreased dramatically among longer-term residents in the UK (Constantine et al. 1988).

6.4.2 Study Design

The migrant study groups were first-generation Bangladeshi women who migrated to the UK as adults (ADU = 62), first-generation Bangladeshi women who moved to the UK as children (CHI = 51) and second-generation women of Bangladeshi descent born in the UK (2ndGEN = 34). A group of nonmigrant (sedentee) Bangladeshi women (SYL = 52) and one of white British women living in the same London neighbourhoods as the Bangladeshi women (WHI = 50) were used as references in the comparisons. Except for the occasional short visit to Bangladesh, all first- and second-generation women had lived uninterruptedly in the UK since migration or since birth, respectively. Most participants were neighbours of the boroughs of Tower Hamlets and Camden in London, where the majority of the Bangladeshi population is concentrated (ONS 2012)

Detailed quantitative information on socio-demographic variables, reproductive and migration histories, lifestyle, health and diet was collected through closed-ended questionnaires administered on a one-to-one basis. These data were used to make intergroup comparisons of the social, cultural and biological changes including breastfeeding patterns sequential to the migration experience.

6.4.3 Comparison of Breastfeeding Patterns Among Immigrant Groups

Results show that breastfeeding incidence, calculated as the proportion of study participants' offspring who were ever breastfed, is the highest for the Bangladesh-born offspring of adult immigrants (100 %; some participant women already had children at the time of migration). No significant differences in incidence of breastfeeding were found between babies born in the UK to either group of first-generation immigrants (range 76–83 %). Adult immigrant women who gave birth in both countries were less likely to breastfeed their UK-born than Bangladesh-born babies (76 versus 100 %, respectively; Fig. 6.3). For all immigrant groups, neither number of years of education nor the mother's age among primiparae women affected breastfeeding incidence.

The duration of breastfeeding was measured as the length of time (in months) for which breastfeeding continued. There were no significant differences in breastfeeding duration among UK-born offspring of women of all three immigrant groups (range 7.8–4.8). However, adult immigrants who gave birth in Bangladesh breastfed their offspring on average twice as long as Bangladeshi women who gave birth in the

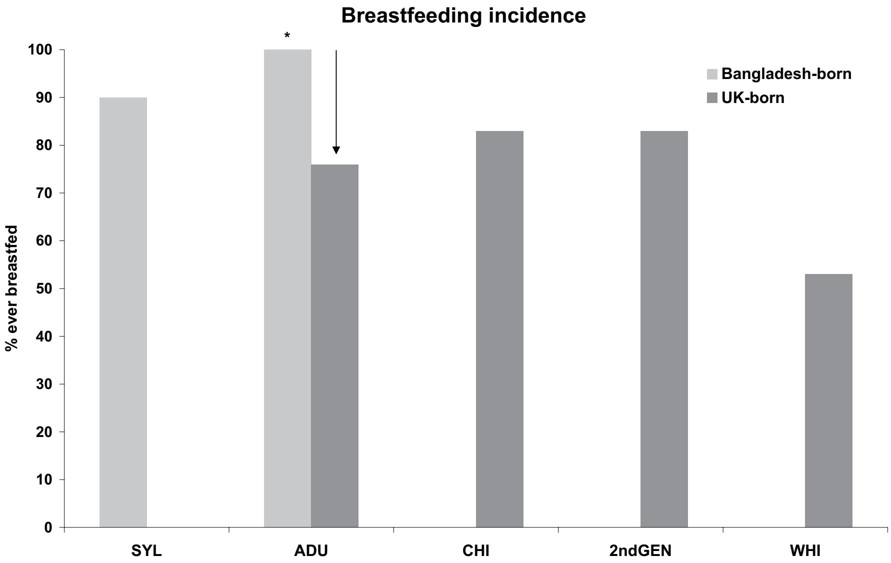

Fig. 6.3 Breastfeeding incidence per migrant study group. Incidence of breastfeeding refers to the proportion of infants who were ever breastfed (% of all live births). A total of 376 infants were born to: nonmigrant (sedentee) Bangladeshi women (SYL = 28), first-generation Bangladeshi women who migrated to the UK as adults and gave birth in the UK (ADU UK = 166), first-generation Bangladeshi women who migrated to the UK as adults and gave birth in Bangladesh (ADU BAN = 51), first-generation Bangladeshi women who moved to the UK as children (CHI = 72), second-generation women of Bangladeshi descent born in the UK (2ndGEN = 30) and white British women living in the same London neighbourhoods as the Bangladeshi women (WHI = 29). Adult immigrant women who gave birth in both countries were less likely to breastfeed their UK-born than Bangladesh-born babies. $*p < 0.05$

UK (Fig. 6.4). For example, within-subject comparisons show that Bangladesh-born children were breastfed on average 10 months longer than their UK-born siblings.

Although average differences in breastfeeding duration between immigrant groups living in the UK were not significant, data on breastfeeding prevalence at different ages reveal contrasting patterns between groups of women. Breastfeeding prevalence was taken as the proportion of all babies who were wholly or partially breastfed at specific ages. In the sample, the proportion of women who breastfed for more than 15 months among first-generation immigrants in London was 23 and 22 % for adult and child immigrants, respectively, compared to only 6 % among second-generation women (contrast with 41 % for sedentee women in Bangladesh and 8 % for the white women group; Fig. 6.5; for detailed statistical analyses, see Núñez-de la Mora 2005).

In summary, the findings, although limited owing to small sample sizes, argue for an important modification in breastfeeding patterns among Bangladeshi immigrants in the UK. The most apparent change is not in the overall incidence but rather

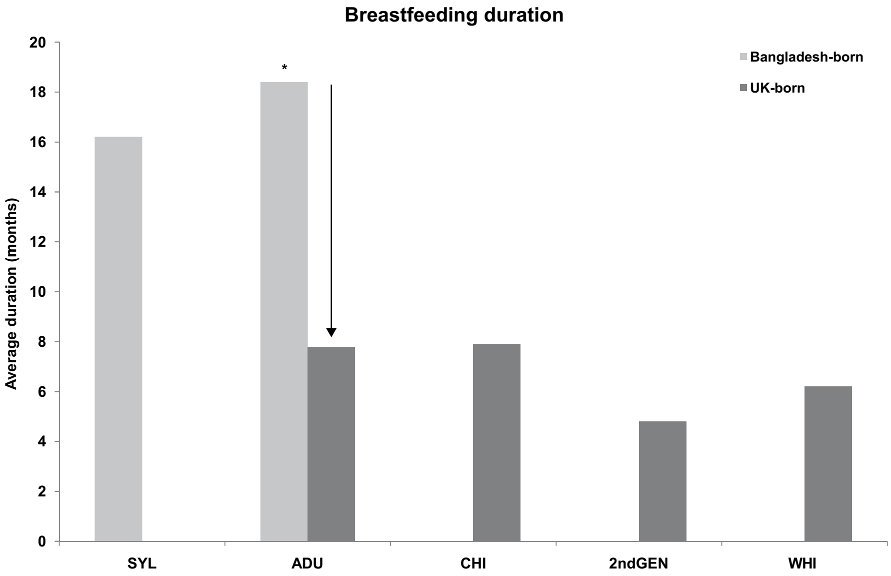

Fig. 6.4 Duration of breastfeeding per migrant study group. Duration of breastfeeding refers to the average length in months for which breastfeeding continued at all, regardless of when other milk and foods were introduced. N = 376 infants (SYL = 28, ADU UK = 166, ADU BAN = 51, CHI = 72, 2ndGEN = 30, WHI = 29). See legend of Fig. 6.3 for description of study groups. Adult immigrants who gave birth in Bangladesh breastfed their offspring on average twice as long as Bangladeshi women who gave birth in the UK. *$p < 0.05$

in the reduction in average duration and prevalence of breastfeeding among British-born Bangladeshi women.

6.4.4 Discussion

Overall, the evolutionary model predicts that in Bangladesh where conditions are insalubrious, infectious disease is widespread and infant mortality risk is high, breastfeeding duration will tend to be long. In the UK, the experience of improved sanitary conditions, lower disease risk and higher caloric diets among immigrants is expected to result in shorter breastfeeding duration either through earlier supplementation and/or weaning as compared to Bangladesh. Finally, for British women whose baseline is an environment of energy surplus and low pathogenicity, breastfeeding duration is expected to fall in the lower end of the spectrum.

The findings for maternal behaviour from the Bangladeshi migrant study fit these predictions rather nicely; quantitative data show a reduction not only in breastfeeding duration among immigrant women but also in the proportion of them who are still breastfeeding past 6 months (Fig. 6.5). Most interestingly, among immigrant

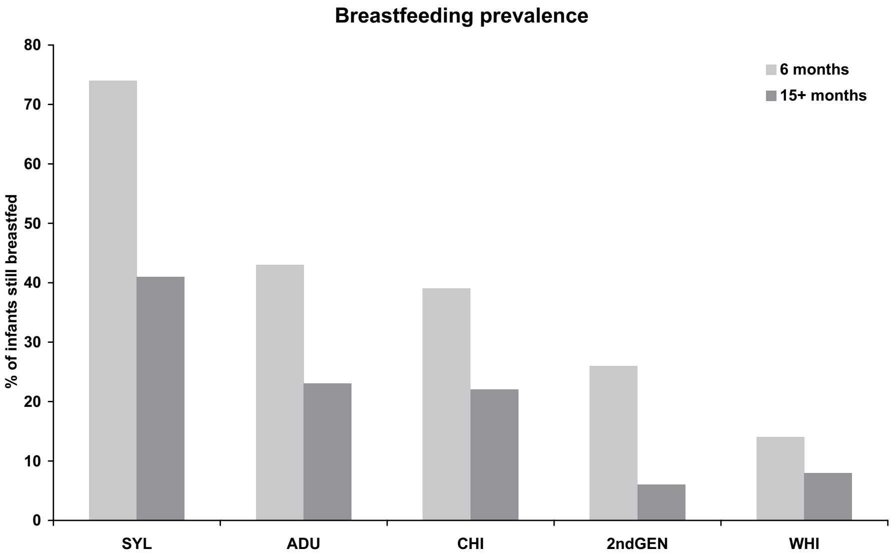

Fig. 6.5 Prevalence of breastfeeding per migrant study group. Prevalence of breastfeeding refers to the proportion of all children who were wholly or partially breastfed at specific ages (% of infants still breastfeeding at 6 and 15 months). N = 376 infants (SYL = 28, ADU = 217 (including ADU UK and ADU BAN), CHI = 72, 2ndGEN = 30, WHI = 29). See legend in Fig. 6.3 for description of study groups. First-generation immigrants were almost four times more likely to continue breastfeeding at 15 months than their second-generation counterparts

women who birthed in both countries, breastfeeding duration coincides with the pattern predicted for the corresponding local ecology: long in Bangladesh and short in the UK.

As a whole, the conclusion of this exercise supports the idea that breastfeeding is a flexible behaviour that evolved to adapt to changes in the local conditions in ways as to maximise trade-offs for both, mother and infant.

6.5 Implications for Public Health

As mentioned at the beginning of this chapter, the issue of declining breastfeeding rates among immigrant and ethnic minority populations has been addressed before, motivated to a large extent by the negative impact of such changes on maternal and infant health and the potential consequences for health-care provision and economics (Bartick and Reinhold 2010). With a goal to inform policy, social scientists and public health specialists have concentrated their efforts on identifying the cultural beliefs and practices that favour or constrain healthy breastfeeding behaviour, as well as the barriers that immigrant women experience when seeking services, including language barriers, discrimination and conflicting belief systems (Hoddinott and Pill 1999; Ingram et al. 2008; Ingram et al. 2003; Twamley et al. 2011; Womens Health and Family Services 2007; Woollett et al. 1995). Overall, the findings of such work highlight the contradictions and conflicts that immigrants experience in their new socioeconomic and cultural reality and, typically, interpret deleterious behavioural shifts as a negative consequence of acculturation and radical changes in lifestyle (Schmied et al. 2012). Moreover, many of these studies make recommendations that imply that such 'undesirable' trends can be reversed and place the emphasis on designing culturally sensitive interventions and policies that remove at least some of the barriers that preclude women from breastfeeding according to their cultural norm (Woollett et al. 1995).

Although some success stories attest to the potential of such culturally sensitive interventions for improving breastfeeding rates (Abramson 1992; Janssen et al. 2009; Wright et al. 1997), the evolutionary model developed in this chapter predicts a rather more pessimistic scenario, not only for immigrant groups but also for other populations in transition. Specifically, the model predicts that the cues of the social and ecological environment in the host countries, particularly in relation to the perceived low risks of infant mortality and morbidity, are likely to be at odds with the public health message in favour of the enhanced survival and health benefits of prolonged lactation. Moreover, some initiatives that aim, in principle, to eliminate some of the structural constraints associated with reduced breastfeeding may in fact directly or indirectly impact maternal opportunity costs and accentuate trade-offs in favour of early supplementation and weaning. Following this argument, the trends in breastfeeding rates in relatively affluent societies are expected to remain relatively low unless novel selective pressures in the physical and sociocultural environment tilt the cost/benefit equation back in favour of prolonged breastfeeding (McDade and Worthman 1998).

This less than hopeful view from the standpoint of evolutionary anthropology should by no means be understood as a condemnation of all breastfeeding promotion programmes to failure and a call for these to be abandoned. After all, breastfeeding for a short period is better than none for both, mothers and infants. Instead, the intention is to emphasise the need for strengthening aspects of such programmes related to advanced weaning and increased fertility rate, both predicted to result in shortened breastfeeding duration among immigrants in affluent settings.

Healthy weaning is contingent upon safe, nutritionally adequate foods fed to the infant in right amounts (Marriott et al. 2012). Complementary foods low in micro- and macronutrients and/or caloric content may result in undernutrition, anaemia and increased susceptibility to infectious disease (Lutter and Lutter 2012; Przyrembel 2012). Similarly, an unbalanced complementary diet of nutritionally poor and energy-dense foods may not only result in overweight and malnourished infants but also set them on a path of high risk of chronic disease for life (Hornell et al. 2013; Robinson and Fall 2012). These two scenarios are not exclusive but can, in fact, occur simultaneously even in populations in developed countries (Caroli et al. 2012).

Findings from large-scale feeding surveys indicate that in the UK, one-fifth of non-white and one-third of white mothers have introduced solids by 4 months of age or earlier (Griffiths and Tate 2007); indeed, a quarter of them have done so by the age of 8 weeks (Foster et al. 1997) and, by 6 months, 99 % of all mothers have fed infants foods other than breast milk, irrespective of their ethnic background (NHS 2011). In terms of the adequacy of the weaning diet, the most recent survey on infant feeding practices indicates that the majority of the white population met the dietary recommendations for children aged 4–18 months, while non-white children of similar age were more likely to be given at least one nutritional supplement during the survey (UK Department of Health 2011). The suggestion that non-white infants may have compromised complementary diets is also evident in an earlier report that found infants of South Asian origin more likely to consume sugary foods during infancy (Williams and Sahota 1990).

These statistics indicate that the supplementation earlier than the WHO-recommended age of 6 months is highly prevalent in the UK population, including the ethnic minority groups, as predicted. Although insufficiently documented, there are signs of inadequate practices in the latter that are cause for concern. Such a disadvantage is in line with the argument developed in this chapter, and calls for greater emphasis on health education and promotion initiatives to improve complementary feeding practices among the UK immigrant communities.

Maternal fertility is another element discussed in the context of this evolutionary that ought to be considered in health promotion efforts. With a trend towards reduced breastfeeding lengths, early infant weaning and in a background conducive to robust fecundity, immigrant women's risk of closely spaced births increases. Although reproductive decisions are not solely dependent on biological factors, this increased reproductive potential highlights the need for adequate family planning during the postpartum period and calls for relevant programmes to be strengthened and delivered alongside postnatal general health and infant feeding advice, particularly as some immigrant communities show some of the highest total fertility rates in the UK (ONS 2012).

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Chapter 7
The Evolutionary Demography of Sex Ratios in Rural Bangladesh

Mary K. Shenk, Mary C. Towner, Kathrine Starkweather, Curtis J. Atkisson and Nurul Alam

Abstract In this chapter, we use evolutionary models of sex ratio variation to examine offspring sex ratios in Matlab, Bangladesh, from the 1960s to 2010, during which time sex ratios have shown a decreasing male bias. Evolutionary models lead us to examine particular aspects of family ecology, yielding predictions both unique from and similar to those proposed in the demographic literature. We examine three evolutionary models—the costs of reproduction model, the Trivers–Willard hypothesis, and the local resource competition and enhancement models. Our results support both the Trivers–Willard and local resource competition/enhancement model, but results for the costs of reproduction model are weak. In general, we find that variables associated with higher wealth, status, and engagement in agriculture are linked to more male-biased offspring sex ratios, while higher fertility, older age at marriage, and higher women's education are associated with less male-biased sex ratios. We also examine how Bangladesh fits into the larger cultural area of South Asia known in the press and policy circles for its high sex ratios. We compare the correlates of sex ratio in Matlab to those in other parts of the region and discuss why sex ratios in Bangladesh are less male biased, despite shared cultural characteristics, such as son preference and dowry, which some argue "cause" high sex ratios in parts of India and Pakistan. We conclude with a discussion of the utility of evolutionary models and offer policy recommendations for the region.

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7.1 Introduction

Male-biased sex ratios and parental behaviors meant to manipulate child sex ratios raise controversial ethical questions and generate complicated cross-cultural debates on public policy, public health, and gender equity. Perhaps no part of the world is a better example of this dynamic than modern South Asia. This area is well known for its male-biased sex ratios, strong cultural norms of son preference, and various forms of discrimination against daughters. Less commonly recognized, however, is sex ratio diversity within South Asia itself—although many areas have strongly male-biased sex ratios, others are more balanced. Some of these regional differences are linked to social and economic distinctions, yet the causes of sex ratio variation on a regional scale are often difficult to ascertain.

Bangladesh is in some ways an anomaly. The country has a long history of cultural practices associated with male-biased sex ratios in India, Pakistan, and China, including patrilineal inheritance, patrilocal residence, a strongly male-biased labor force, relatively low levels of female education, rapid economic development and urbanization, and rising dowry costs (Arnold et al. 1996; Clark 2000; Das Gupta and Bhat 1997; Das Gupta et al. 2003; Echavarri and Ezcurra 2010; Edlund 1999; Guilmoto 2009; Hesketh and Xing 2006; Murthi et al. 1995). A sex ratio of 105 males to 100 females at birth is considered normal. In Bangladesh, the sex ratio at birth in 2011 was 104, a low (unbiased) number similar to regions of South Asia, such as Sri Lanka, Nepal, or Kerala State in India, and in stark contrast to some regions of India or Pakistan where sex ratios can be as high (male biased) as 120 (United Nations 2011; see Table 7.1). In fact, there has been a noticeable *decline* in sex ratios in rural Bangladesh in the past two decades, during a period when sex ratios in much of North India have been rising. Studies on sex ratio in Bangladesh are very limited, however. Although some statistics have been reported (e.g., International Centre for Diarrhoeal Disease Research, Bangladesh (ICDDRB 2012b), they have not been explored in terms of patterns and correlations.

Clark (2000) used a family-level approach to explore son preference in India according to socioeconomic status (SES) and region. Otherwise, most sex ratio analyses published in the demographic literature take place at the population level, with comparisons made between states or countries (e.g., Guilmoto 2009; Miller 1989). Population measures of sex ratio give us aggregate measures across a large number of families during a particular time period and for a particular age group. While such aggregate statistics are useful in describing population trends, they can conceal differences between families and trends occurring within or across families over time. To fill this gap in the literature, we analyze sex ratio at the level of the family, testing the degree to which offspring sex ratios match predictions from the evolutionary literature. A similar approach has been used to study sex ratio variation in non-human animals, for instance in bird clutches (e.g., Krakow and Tkadlec 2001). Evolutionary approaches to sex ratios spotlight parental investment strategies in particular, asserting that when one sex of offspring out-earns the other, or costs more to raise, or when only children of one sex inherit or take care of parents

Table 7.1 Sex ratios in South and East Asia

Region	Sex ratio[a]	Age range	Years	Source
East Asia				
China	118	Birth	2010	Hudson 2011
	110.2	1–5 years	1990	Coale and Banister 1994
Tibet	97–107	Birth	2005	Li 2007
Hainan	122	Birth	2005	Li 2007
Shanghai	120	Birth	2005	Li 2007
Guangdong	138	Birth	2000	Li 2007
Korea	112.5	Birth	1990	Park and Cho 1995
	111.4	4 years	1990	Park and Cho 1995
Taiwan	109.1	Birth	1990	Park and Cho 1995
	106.6	4 years	1990	Park and Cho 1995
Japan	104.9	0–4 years	2000	Census of Japan 2005
	104.8	0–4 years	2005	Census of Japan 2005
South Asia				
India	108.6	Birth	2011	Census of India 2011
	109.4	0–6 years	2011	Census of India 2011
Punjab	118.2	0–6 years	2011	Census of India 2011
Haryana	120.5	0–6 years	2011	Census of India 2011
Kerala	104.3	0–6 years	2011	Census of India 2011
Chhattisgarh	103.7	0–6 years	2011	Census of India 2011
Meghalaya	103.1	0–6 years	2011	Census of India 2011
Pakistan	105	Birth	2010	CIA Factbook 2012
	106	0–14 years	2010	CIA Factbook 2012
Nepal	94	0–4 years	1971	Nepali National Population Census 2011
	104.9	0–4 years	2011	Nepali National Population Census 2011
Sri Lanka	104.3–105.2	Birth	1985–1988	Abeykoon 1995
	104	Birth & 0–15	2012	CIA Factbook 2012
Bangladesh	104	Birth	2011	CIA Factbook 2012
	103	0–14 years	2011	CIA Factbook 2012
	102	Birth	2010	ICDDRB Workbook 2012b
Matlab	103.4	0–4 & 5–9	2006–2010	ICDDRB Workbook 2012b

[a] Sex ratio is read as the number of boys per 100 girls. Other notations for sex ratio exist, including number of girls per 1,000 boys (commonly reported in India)

in old age, parents use this information to make strategic decisions to favor the more beneficial or less costly sex (Hrdy and Judge 1993).

Our aims in this chapter are twofold. First, we evaluate whether evolutionary models of sex ratio variation explain patterns of offspring sex ratio in Matlab, Bangladesh. Some predictions are similar to those proposed in the demographic literature, but some are unique. We then test our predictions to see (a) whether the relevant variables have the expected effect on sex ratio and (b) whether particular evolutionary models are more important than others in understanding offspring sex ratios. Second, we examine how the Bangladeshi case fits into the larger cultural area of South Asia, known in the press and policy circles for its high sex ratios. We discuss which correlates of sex ratio are similar to those in other parts of South Asia and which are not, and why sex ratios in Bangladesh differ despite sharing many cultural characteristics, such as son preference and dowry, thought to "cause" high sex ratios in other parts of the subcontinent. We conclude with a discussion of the efficacy of evolutionary models and by offering several public policy recommendations for Bangladesh and the region as a whole.

7.1.1 Mechanisms of Sex Ratio Variation

Among humans, a "natural" sex ratio at birth has consistently been reported as 105 males to females, i.e., for every 100 females born, around 105 males are born (Coale 1991). Cross-culturally, a sex ratio that falls within the range of 104–107 is generally considered normal (Chahnazarian 1988). The sex ratio at birth (also known as the secondary sex ratio, the primary sex ratio being the sex ratio at conception) is determined in large part by two biological mechanisms: sex determination at conception and spontaneous abortion during gestation. There is some evidence that the mother's health and nutritional condition affect the sex of a fetus (Cameron 2004; Zhou 2007), as well as some evidence for sex-specific mortality in utero (Catalano et al. 2005; Navara 2010). These findings suggest that women in better health give birth to more boys than do women in poorer health, although the mechanisms that underlie the relationship are not well understood. Other factors, such as coital frequency (James 2009) and hormonal concentrations of parents at the time of conception (James 2012), may also affect sex ratio at birth. For example, James (2009) and others have argued that there are higher male sex ratios at birth during and after wars, an effect possibly driven by coital rates.

Several mechanisms are thought to be largely responsible for the biased sex ratios at birth or within the first years of life in many parts of Asia (Das Gupta and Shuzhuo 1999). Preferential female abortion has been reported in areas where son preference is high and technology is available to determine the child's sex before birth (Das Gupta and Bhat 1997; Echavarri and Ezcurra 2010; Hesketh and Xing 2006). Where such technology is not available, however, parents can bias the sex ratio of their offspring through intentional neglect of daughters leading to higher female mortality (Hesketh and Xing 2006; Miller 1989). Additionally, Park and Cho (1995) suggest that parents can affect the sex ratio of their offspring through differential contraceptive use, which may be especially important when family sizes are moderate and parents can use contraceptives to stop reproduction after the birth of a son. Although infanticide occurred in India (Dickemann 1979) and elsewhere in Asia in the past (Guilmoto 2009), and is often unreported (Das Gupta and Bhat 1997), it appears to be rare in recent years (Guilmoto 2009; Hesketh and Xing 2006; Park and Cho 1995), and thus is not likely to be a significant cause of contemporary sex ratio bias.

Sex ratio at birth is important for understanding biological differences between populations including population responses to stress and forms of sex ratio manipulation which occur before birth, such as sex-selective abortion. To better understand sex ratio manipulation of the type reported to be common in South Asia, however, sex ratios among older children more closely reflect sex ratio *after* any parental modifications have been made. For these reasons, we examine sex ratio among children surviving to age ten, the earliest age at which children begin to adopt adult roles including working outside the home, labor migration, and marriage, though most children do not experience these events until older ages. Many demographers investigate sex ratios among children aged 5 or older to study the impact of different types of sex ratio manipulation occurring after birth (e.g., Clark 2000; Das Gupta and Shuzhuo 1999; Miller 1989). Additionally, studying child sex ratios reflects an emphasis on comparative parental investment strategies in behavioral ecology and evolutionary demography.

7.1.2 Evolutionary Explanations

Typical explanations of biased sex ratios in the demographic literature focus on cultural constructs such as son preference or female empowerment, but these proximate explanations do not answer the question of *why* differences in parental investment or gender roles exist to begin with. Evolutionary approaches, in contrast, focus on ultimate explanations which attempt to understand the root cause of a phenomenon in terms of behavioral strategies meant to result in higher fitness. An evolutionary approach can connect proximate explanations to an overarching theoretical framework (e.g., Clarke and Low 2001). Evolutionary theories of sex ratio and sex-biased investment suggest reasons for why son preference may be so prevalent cross-culturally and the circumstances in which it is most likely to exist, as well as why empowered women have children with more equal sex ratios (Hrdy and Judge 1993).

Our work falls squarely into the field of evolutionary demography (e.g., Clarke and Low 2001), combining demographic data and research questions with evolutionary models and drawing on methods from both fields. Evolutionary theoretical models typically show how similar ecological circumstances give rise to predictable outcomes, allowing us to generalize about how an underlying process will play out in different contexts. In contrast, studies in public policy or demography typically examine many variables to identify those of interest in a specific context; they may or may not refer to an underlying theoretical framework. We argue that these approaches can be usefully combined by constructing and comparing models that include both evolutionary predictors and key contextual variables to gauge their relative importance.

7.1.3 Sex Ratio in South Asia

There is tremendous variability in sex ratios throughout East and South Asia, running counter to the popular media portrayal of uniformly high male bias. Here, we introduce the variation in and correlates of sex ratio in the region (Table 7.1).

In India, the sex ratio has been steadily increasing over the past 40 years. Even so, the nationwide sex ratio of 109.4 for ages 0–6 is still only moderately higher than the normal range of sex ratio variation (Chahnazarian 1988). In fact, it is not the nationwide average that has garnered significant attention, but the very high sex ratios in some states in northern India (Arnold et al. 1996; Clark 2000; Das Gupta 1987). In the state of Punjab, for instance, the sex ratio for ages 0–6 is currently 118, but has rarely dipped below 110 over the past 40 years. This represents the extreme end of a trend that incorporates many Indian states, thought to be the result of decreasing female child survival, a trend that runs counter to the increasing survival found in other parts of the country (Agnihotri 1995, 2000).

Son preference is a strong norm across South Asia and many see it as the catalyst behind high sex ratios in the region (Das Gupta and Bhat 1997; Das Gupta and Shuzhuo 1999; Echavarri and Ezcurra 2010; Miller 1981). In other parts of the world where son preference is strong, most notably China and Korea, biased sex ratios are also reported (Johansson and Nygren 1991; Park and Cho 1995). Park and Cho (1995) suggest that the bias in the sex ratio in modern Korea is due to the presence of son preference in a low-fertility society; families have fewer children than in the past, but their preference for sons remains high, leading to behaviors that bias the sex ratio in favor of males.

Both individual and group effects appear to impact son preference. Murthi et al. (1995) report that decreased income and increased education, especially among females, are related to decreased son preference, though the direction of causation is unclear (see also Clark 2000; Echavarri and Ezcarra 2010). Religion and caste are also potential correlates of son preference, especially in India (Clark 2000; Pande and Astone 2007). Hindus and Sikhs are found to have the highest son preference followed by Muslims and finally Christians, while low-status groups such as Scheduled Castes and Scheduled Tribes and people in North India also have higher-than-average son preference (Clark 2000).

Son preference also appears to be related to dowry (Arnold et al. 1996; Clark 2000; Das Gupta et al. 2003; Edlund 1999; Guilmoto 2009). Dowry, which is paid by the bride's family at the time of marriage, is often seen as a financial burden imposed on the family by daughters (Edlund 1999), who typically do not contribute significantly to the family income, especially in rural areas (Das Gupta et al. 2003). Sons, on the other hand, contribute to the family economy in the forms of income from wage labor and dowry paid by their wife's family (Mutharayappa 1997). Therefore, increases in dowry payments may result in increased son preference.

One of the primary proximate mechanisms impacting sex ratio in South Asia appears to be preferential female abortion, especially in places such as India, China, and Korea, where ultrasound technology is readily available (Echavarri and Ezcarra

2010; Das Gupta and Bhat 1997). When there is no access to prenatal sex detection technology, son preference may lead parents to focus instead on having an ideal number of sons, stopping only after the desired number of sons is achieved (Arnold et al. 2002; Clark 2000). Such a strategy becomes problematic, however, with preferences for smaller families (Das Gupta and Shuzhuo 1999; Murthi et al. 1995), and sex-specific neglect may be employed as a way to bias the sex ratio towards sons after birth (Das Gupta 1987; Miller 1981; Rosenzweig and Scultz 1982).

Many regions of South Asia have a sex ratio of 105 or lower (Table 7.1). Low sex ratios are most common in South and Northeast India, areas that are historically matrilineal, practice rice agriculture, and/or have large culturally distinct tribal populations. Sri Lanka and Nepal also have low sex ratios. Sri Lanka shares some cultural features with South India, but Nepal more closely resembles North India including strong traditions of patrilineality and patrilocality. Women in Sri Lanka have higher status than in other parts of South Asia, including higher literacy, education, life expectancy, and participation in economic activities (Abeykoon 1995). To a lesser extent, women in Nepal also have higher status than women in North India do.

Although sex-selective abortion is less common in Bangladesh than in India (Hesketh and Xing 2006), preferential female neglect through food distribution has been reported (Chen 1982; D'Souza and Chen 1980; Miller 1989). Chen (1982) has suggested that differences arise between India and Bangladesh because of the heterogeneity of the Indian population with respect to socioeconomic markers, such as ethnicity, religion, income, and modernization. Yet, while Bangladesh has less socioeconomic and cultural diversity than the much larger India, this does not explain why Bangladeshi sex ratios are similar to some parts of India but not others. Indian regions with low sex ratios, such as Kerala State and Northeast India, for instance, can be quite culturally and religiously diverse.

7.1.4 The Politics of Sex Ratios

In public policy circles, unbalanced sex ratios are usually seen in a negative light, as either a consequence or a cause of social problems. Much attention has been paid to discrimination against daughters through sex-biased abortion, infanticide, and sex-specific neglect, leading to higher female mortality, undernutrition, or morbidity (e.g., Chen 1982; Das Gupta and Shuzhuo 1999; Miller 1981). Also of concern are the social implications of large numbers of unmarried men, including the difficulties individuals and families face if sons are unable to find a marriage partner, have children, or take care of parents and family businesses (Hudson and den Boer 2004). Moreover, some argue that such pressures could lead to rising rates of domestic violence and social conflict (Hudson and den Boer 2004); yet, others have argued that the perspectives of policymakers do not necessarily follow from logically consistent models (Brooks 2012). Moreover, views of unbalanced sex ratios as a social problem can be seen as ethnocentric, since such perspectives often reflect the views of

Fig. 7.1 Women processing rice in Matlab. Both men and women work in the fields, but women are responsible for much of the post-harvest processing of crops in Bangladesh. (Photo courtesy of Mary K. Shenk)

policymakers in developed countries rather than the perspectives of local families facing difficult trade-offs.

7.1.5 Study Population

Matlab, Bangladesh, is a rural area located in Chandpur District. Villagers of Matlab traditionally practiced agriculture(Fig. 7.1), fishing, and small trading (Holman and O'Connor 2004; ICDDRB 2007). Over the past three decades, however, these practices have been changing in response to decreasing land ownership and increasing access to local, national, and international labor markets (Kabeer 2001; Nowak 1993). Bangladesh is also undergoing a demographic transition; between 1966 and 2010, total fertility rates in Matlab fell from 6.7 to 2.6 children per woman (Fig. 7.2). Conversely, life expectancy at birth rose from 53 to 69.3 years for men and from 51 to 73.2 years for women, due mainly to sharp decreases in infant and child mortality (ICDDRB 2007, 2012). There is evidence that in some parts of India, China, and Korea, declining fertility rates are associated with increasing son preference and thus higher sex ratios (Guilmoto 2009; Nie 2009; Sekher and Hatti 2010). This does not appear to be the case in rural Bangladesh, where recent evidence suggests that child gender preference may be shifting towards a higher valuation of daughters (Fraser 2011).

Fig. 7.2 Lower fertility in Matlab, Bangladesh. A family including mother (*left*), father (*right*), grandmother (*rear*), and two daughters. (Photo courtesy of Mary K. Shenk)

Agriculture in Matlab has decreased as a primary occupation, and villagers have increasingly adopted wage labor, largely in construction, transportation, and small businesses. Labor out-migration has also increased, with more men traveling to cities in Bangladesh or abroad to work as laborers, primarily in construction and maintenance, or as domestics (Afsar 2009; ICDDRB 2007; Nowak 1993). Although men who are labor migrants may not be physically present in the household, they usually remain financially and socially connected to their families, sending remittances home to their parents, wives, and children. Educational levels for both men and women are increasing (ICDDRB 2007), though for men, this is much more likely to pay off in the labor market, whereas for women, education is primarily expected to pay off in the marriage market and serves as a backup strategy in case the woman is widowed or divorced.

In rural Bangladesh, families are extended or nuclear and live in close proximity to other kin in a *bari* or patrilineal compound (Aziz 1979). Patrilocal residence and patrilineal inheritance are the norm, with sons staying with or near their parents and daughters marrying into more distant families. Matlab villagers traditionally paid bride-price (a payment from the groom's family to the bride's family at marriage), but now almost exclusively pay dowry (a payment from the bride's family to the groom or groom's family at marriage). This transition has taken place in the past several decades, possibly due to changes in Bangladeshi family law that requires marriage registration, or more generally to economic development, as in other regions of South Asia (Ambrus et al. 2010; Caldwell 2005). Dowries may serve as hedges against divorce, as well as a form of premortem inheritance for women (Ambrus et al. 2010; Esteve-Volart 2004). In wealthier families, daughters obtain higher levels of education and marry at older ages; their families often pay larger dowries to marry their daughters to higher-status grooms (Esteve-Volart 2004). Poorer families may marry daughters early to lower-status grooms in order to avoid burdensome dowry payments, which tend to increase with the daughter's age and perceived risks to her chastity (Caldwell 2005).

Son preference is traditional in South Asia (Das Gupta et al. 2003), including rural Bangladesh. Sons remain economically connected to and responsible for their birth families, including caring for younger siblings, elderly parents, and their own families after marriage. Sons generally bring in the dowry at marriage and may have religious obligations to parents, such as lighting their parents' funeral pyres among Hindus. Daughters, on the other hand, rarely work before marriage in rural Bangladesh. Any income they earn after marriage becomes part of the finances of their husband's family. These norms may be changing, however. Although daughters were always instrumental in helping take care of younger siblings, our qualitative interviews highlight the increasing importance of girls in helping their families, including their aging parents, after marriage. Help from daughters may be especially important if sons and daughters-in-laws are physically absent from the *bari* due to labor migration (Afsar 2009; Fraser 2011).

7.1.6 Evolutionary Models of Sex Ratio

In the past 40 years, both theoretical and empirical studies of human and non-human sex ratios have proliferated in evolutionary ecology (e.g., Cockburn et al. 2002; Kokko and Jennions 2008; Hardy 2002; Sieff 1990). Here, we describe several evolutionary models of sex ratios and the predictions we draw from them for our Matlab sample.

Costs of Reproduction Hypothesis Although Darwin knew that within a species, male and female offspring are typically produced in equal numbers (Darwin 1871), it took until the 1930s for Fisher (1930) to suggest a plausible evolutionary explanation for the phenomenon. Fisher reasoned that males and females should be produced in roughly equal numbers because, as population sex ratio drifts from equality, parents who produce the rarer sex will have higher fitness. Fisher further reasoned that when one sex is more costly to raise (in terms of time, energy, or resources), parents should increase production of the less costly sex such that expenditure on male and female offspring is equal.

Starting in utero, male neonates, and to a lesser degree male infants and children, are more vulnerable to mortality as well as morbidity early in life, especially when infectious diseases and malnutrition are common and modern medical care is limited (McMillen 1979; Waldron 1985). Taken on a per-offspring basis, males may be less costly than females simply because they are, on average, alive for a shorter amount of time. According to the equal expenditure hypothesis, this may explain the male-biased sex ratio at birth (Fisher 1930). This view leads to "Prediction 1: Higher-male neonatal mortality rates should be positively correlated with male-biased sex ratios at birth." We test this using the male neonatal mortality rates in Matlab, Bangladesh, when the woman was 18–20 years old.

Wells (2000) argues that greater intrinsic male vulnerability during gestation, infancy, and childhood could itself be a direct product of natural selection if male and female children offer different returns on parental investment. When environmental conditions are poor, the greater vulnerability of male infants makes them less likely to survive or thrive in conditions that are unfavorable for male children, and those males who do survive will be the ones in better condition. Poor parental condition or poor local conditions should therefore lead to a more female-biased sex ratio among surviving children.

Moreover, despite greater male vulnerability, evidence suggests that for human mothers, producing a surviving male is more costly than producing a female (Mace and Sear 1997; Helle et al. 2002). Males require more caloric investment both in utero and during lactation and even appear to decrease maternal longevity in certain contexts (Helle and Lummaa 2013; Helle et al. 2002). Given such costs of reproduction, mothers are predicted to adjust their offspring sex ratios according to their own ability to bear the costs of producing sons (Gomendio et al. 1990; Myers 1978). Both a mother's current circumstances and the conditions she experienced during development are likely to be important. For example, Gibson and Mace (2003) found that Ethiopian mothers in good condition, specifically those with higher body mass indexes (BMIs) and upper-arm muscle mass, were more likely to have produced a son in their previous birth.

Thus, the framework of the costs of reproduction also leads to"Prediction 2: Offspring sex ratio will be negatively correlated with poor parental or local conditions, as parents find it more difficult to raise sons to adulthood." Specific predictor variables are whether the woman experienced food insecurity when she was herself a child, and the number of child deaths which occurred in the woman's marital bari during the first years of her marriage (excluding her own children).

Trivers–Willard Hypothesis Trivers and Willard (1973) suggest that in cases where parental investment has an impact on an offspring's future reproductive success, the sex of the offspring produced or reared should reflect parental condition (specifically maternal condition in most species). In species where sons in good condition (i.e., nutritional status, health, social status) are able to out-reproduce daughters in good condition, higher-quality mothers are predicted to be more likely to produce or rear sons. Conversely, in species where daughters in poor condition are able to out-reproduce sons in poor condition, lower-quality mothers are predicted to be more likely to produce or rear daughters. In humans, SES is an important attribute of parental condition and ability to invest in offspring, and although Trivers and Willard originally focused on the sex ratio at birth, they suggested that their model could also apply to postnatal investment. Trivers and Willard (1973) also recognized that paternal investment will reduce variance in male reproductive success relative to females. They argued that the model should still hold, however, if males in higher SES families out-reproduce their sisters, while females in low SES families out-reproduce their brothers.

The Trivers–Willard hypothesis has inspired significant research attention in humans and other primates (see Hrdy 2000, for an overview), with mixed results that have themselves inspired methodological critique (Brown 2001; Lazarus 2002; Towner and Luttbeg 2007). For example, Borgerhoff Mulder (1998) found that higher-status fathers produce more sons than lower-status fathers among the polygynous Kipsigis. And Cronk (2000) and Koziel and Ulijaszek (2001) found evidence that Mukogodo mothers in Kenya and mothers in Poland, respectively, may engage in sex-biased breastfeeding patterns consistent with the Trivers–Willard hypothesis. In contrast, Keller et al. (2001) found no evidence that high-status families have more sons or low-status families have more daughters in contemporary USA and argued that resource allocation rather than sex ratio may be a more relevant measure of parental investment. Methodological issues in detecting Trivers–Willard effects are additionally complicated by potential publication biases (Festa-Bianchet 1966), small sample sizes (Brown and Silk 2002), and a focus on null hypothesis testing (Towner and Luttbeg 2007).

The Trivers–Willard hypothesis leads to "Prediction 3: Wealthier, higher-status families will have higher offspring sex ratios than poorer, lower-status families." Based on ethnographic data and observations, we use the variables household income, woman's education, husband's education, and whether the husband is a labor migrant as proxies for wealth and social status in Matlab.

Local resource enhancement and competition The local resource enhancement and Local Resource Competition models are two sides of the same evolutionary coin—one focusing on cooperation and the other on conflict. The local resource enhancement model proposes that if cooperation among offspring of one sex reduces the costs or increases the benefits of raising offspring, then the sex ratio should be biased towards the cooperating sex (Emlen et al. 1986; Flinn 1988; Turke 1988); local resource enhancement can also occur if offspring of one sex enhance the mating success of parents or siblings (Sieff 1990). The local resource competition model functions similarly; when there is competition among offspring of one sex for resources, the cost of raising offspring of that sex will increase, and parents should bias the sex ratio in favor of the less competitive, less costly sex (Clark 1978; Silk and Brown 2008).

A number of studies have shown the importance of philopatry on local resource competition in mammals, including primates (e.g., Johnson 1988; Silk et al. 1981; van Schaik et al. 1989). In humans, marital residence patterns do not necessarily determine the extent of within-sex competition (Borgerhoff Mulder 1998), but some support exists for local resource models. Borgerhoff Mulder (1998) and Mace (1996) found evidence of competition for resources among inheriting Kipsigis and Gabbra brothers. Quinlan et al. (2005) found that in Dominica, daughters cooperate with mothers in household tasks, freeing mothers to invest in younger children. Consistent with the local resource enhancement model, these mothers breastfeed daughters longer than sons (see also Bereczkei and Dunbar 2002). Hill and Kaplan (1988) suggest that one explanation for the high sex ratio among the Ache in lowland South America might be that sons are less costly to raise because they make a larger contribution to the family's food resources beginning around age of 16 (see also Smith and Smith 1994).

The local resource enhancement model leads to "Prediction 4: Families in which the labor of sons is able to contribute more directly to family resources should have higher sex ratios." Sons in South Asia are very important to kin in terms of income, social support, and care in old age. In particular, sex ratios should be high for sons in agricultural families where the labor of sons is the key means of generating an income. Both land ownership and whether the family works in agriculture serve as measures of the likelihood of local resource enhancement. The local resource competition model leads to “Prediction 5: Daughters compete for resources when dowries are paid. Thus, families which expect to pay higher dowries should have higher sex ratios.” Since not all daughters are married yet, we use the mother’s dowry as a measure of dowry expectations.

7.2 Methods

7.2.1 Data

Results reported here are drawn from a detailed survey of 944 women aged 20–64, conducted in 2010 in Matlab, Bangladesh. The study area includes a population of approximately 250,000 people on whom detailed demographic data have been collected since 1966 as part of the Health and Demographic Surveillance System (HDSS) run by the ICDDRB, a public health and demographic research organization which has worked in the Matlab area for 50 years. Our sample was drawn randomly from a list of all women aged 20–64 living in the HDSS sample area. Even numbers of women were drawn from three 15-year age categories (20–34, 35–49, and 50–64) allowing for better representation of older women since rapid population growth in the Matlab area has resulted in larger cohorts of younger women. Our sample thus allows for 45 years of time depth.

Our survey covered topics including family demographics, education, marriage, occupation, income, migration, health, and risk. Surveys were conducted via interview in the woman’s *bari* and took around 1 hour to complete. We focused our analyses on all women in our survey married for at least 5 years and for whom data were complete on our variables of interest ($N = 795$). Our sample excludes 63 unmarried women (all of whom are childless) and 73 women who have been married less than 5 years (many of whom are childless or only have one child). Only 12 women were excluded because of missing data in one or more variables; there were no clear patterns among these women likely to affect analyses. Summary statistics for all variables analyzed are shown in Table 7.2.

Our analyses focus on the children of women in the sample, simultaneously modeling two dependent variables: the number of boys and the number of girls born and who either survived to age 10 or were alive at the time of the survey in 2010. We count only birth children, excluding stepchildren and adoptees. In rural Bangladesh, it is rare for children to leave the household until they are teenagers so the majority of these children are living at home; fostering is not common except in cases of parental death. Although not all children had yet survived to age ten in 2010, we did not expect censoring to bias our results given that current fertility and mortality rates are comparatively low. Completed family sizes are currently two to three children (in 2010, the average total fertility rate (TFR) was 2.6; ICDDRB 2012a). Based on 2010 mortality rates for children aged 0–1, 1–4, and 5–9 in the

Table 7.2 Summary statistics for women in our Matlab sample

Variable	*N*	Mean	Standard deviation	Median	Range
Dependent variables					
Number of surviving sons	795	1.9	1.26	2	0–6
Number of surviving daughters	795	1.7	1.26	2	0–7
Continuous variables					
Woman's age at marriage (years)	795	16.2	2.93	16	11–33
Woman's age (years)	795	43.7	11.26	44	21 to 67
Household income (Taka per year, logged)	795	11.1	1.05	11.2	6.7–14.9
Husband's education (years)	795	4.8	4.43	5	0–16
Woman's education (years)	795	3.6	3.69	3	0–16
Value of woman's wedding gifts (logged)	795	4.9	5.07	0	0–13.3
Child deaths in marital bari (number)	795	1.6	1.87	1	0–15
Male neonatal mortality rate (deaths per 1,000)	795	62.4	17.8	63.5	20.7–95.7
Categorical variables					
Husband's location			Woman's fertility		
1 = Bangladesh	706		1 = low (4 births or less)		517
2 = Abroad	89		2 = high (5 or more births)		278
Family engaged in agriculture			Whether woman lost a child		
0 = no	407		0 = no		581
1 = yes	388		1 = yes		214
Family owns land			Food insecurity		
0 = no	204		1 = always had enough food		520
1 = yes	591		2 = did not always have enough food		275

Matlab area (ICDDRB 2012a), along with the ages of the children 9 and under included in our dataset, we estimated that at most only 9.5 of the children included in our analyses might die by age 9. Moreover, for these deaths to affect our overall results, there would need to be enough bias among the dead children to change the results for the full sample of 2,853 children.

The predictor variables used in this chapter are listed in Table 7.3. Age, age at marriage, and whether the woman had high or low fertility are considered control variables and are included in all models, including a base model with no other variables. The other predictor variables are related to the evolutionary models being tested (see above). Most predictor variables are from the time before the couple had children—this means that their effects can more plausibly be interpreted as causes of sex ratio rather than simply correlates of it.

Table 7.3 Bivariate relationships between offspring sex ratios and predictor variables

Variable	Levels	Surviving sons	Surviving daughters	Sex ratio (in subset)
Full sample		1,487	1,366	108.9
Woman's age at marriage	Under 15	690	604	114.2
	15–17	540	489	110.4
	18 and over	257	273	94.1
Woman's age	Under 40	358	356	100.6
	40–49	416	398	104.5
	50 and over	713	612	116.5
Woman's fertility	Low	739	642	115.1
	High	748	724	103.3
Household income	Low	444	462	96.1
	Medium	518	462	112.1
	High	525	442	118.8
Husband's education (years)	0	527	502	105.0
	1–5	445	388	114.7
	6 or more	515	476	108.2
Husband's location	Bangladesh	1,366	1276	107.1
	Abroad	121	90	134.4
Woman's education (years)	0	551	446	124.5
	1–5	601	579	103.8
	6 or more	333	345	96.5
Food insecurity	No	959	869	110.4
	Yes	528	497	106.2
Family engaged in agriculture	No	650	630	103.2
	Yes	837	736	113.7
Value of woman's wedding gifts	None	842	786	107.1
	<10.2	361	346	104.3
	≥ 10.2	284	234	121.4
Child deaths in marital bari	0	405	418	96.9
	1 or 2	640	574	111.5
	3 or more	442	374	118.2
Male neonatal mortality rate	Low	326	306	106.5
	Medium	481	469	102.6
	High	680	591	115.1
Whether woman lost a child	No	1,029	922	111.6
	Yes (1 or more)	458	444	103.2

Some women in our sample had likely not yet completed their fertility in 2010. To deal with this, we controlled both age and age at marriage in all analyses. We also removed unmarried women and newlyweds from the sample, excluding the women most likely to be below their completed fertility. Given that completed family sizes are currently two to three children (in 2010, the average TFR was 2.6; ICDDRB 2012a), and that most women marry in their late teens or early twenties and have children soon afterwards, we calculated that likely around 80% of the women in our sample have completed fertility.

All data were collected in accordance with human subjects research protocols approved by the institutional review boards at both the University of Missouri and ICDDRB. All research participants gave informed consent prior to data collection.

7.2.2 Analysis

Sex ratios within sibships or litters are sometimes analyzed as proportions, but this approach is problematic (Warton et al. 2011), as having 100 % sons means something very different for a woman with two children than a woman with six. Instead, we use generalized linear modeling (GLM) based on a binomial probability distribution (Wilson and Hardy 2002; Crawley 2005). Our dependent variable, which we refer to as offspring sex ratio, is a pair of values for each woman: number of surviving sons and number of surviving daughters, allowing us to model sex ratio in a manner which simultaneously accounts for the number of children. We identified 14 independent variables to evaluate as covariates in our model. All analyses were completed using R Development Core Team (2012) and the multi-model inference (*MuMIn*) package (Barton 2013).

We use an information-theoretic approach (Burnham and Anderson 2002) to compare the evidence for alternative models and evaluate the importance of the independent variables in explaining sex ratio variation across women. This type of approach centers on the likelihood of each model given the data rather than null hypothesis testing (see Towner and Luttbeg 2007, for a review, with examples from sex ratio studies; see also Richards et al. 2011). Model comparison relies on Akaike information criterion (AIC) or variations thereof. For a given model, AIC $= -2\log(L) + 2K$, where L is the likelihood of the model given the data, and K is the number of parameters in the model. In this analysis, we use a variation known as quasi Akaike information criterion (QAIC), which adjusts for overdispersion in the data (when the values of the dependent variable are non-independent; Richards 2008). We find a mild degree of overdispersion in our data ($\hat{c} = 1.2$).

Our full model contains 14 covariates (including the three control variables in the base model). All possible subsets of this full model were constructed to calculate each model's QAIC value. Independent variables were assessed based on the number of top models in which they appear, as well as by the weight of those models, with the weight being a measure of the likelihood of that model among those being compared. For each variable, importance values are calculated as the sum of the weights of the models in which that variable appears (Table 7.3). Although a single best model (the model with the lowest QAIC) results from an exhaustive search, a number of models often have similar weights. We therefore used model averaging to construct a model that incorporated information from multiple top models. We followed the recommendations of Richards (2008) in estimating the averaged model, using all models with a $\Delta \le 6$, where Δ is the difference between the model's QAIC value and the lowest QAIC value. We also filtered out all models that were more complex versions of a model with a lower QAIC value, with a further restriction that the control variables were retained in each model.

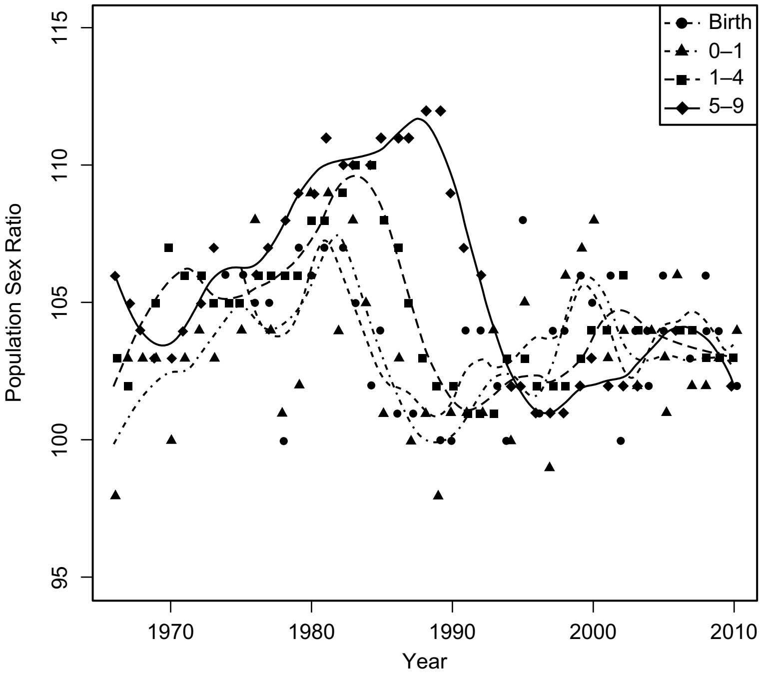

Fig. 7.3 Population level sex ratios for Matlab from 1966–2010. Points show the sex ratio for a given age range in a given year. Lines show the change in the sex ratio of four age categories (birth, 0–1, 1–4, and 5–9) over time. Lines were constructed through loess regression using a span of 0.25. The line for the sex ratio at birth begins in 1974 because birth data were not gathered before that. The trends include a sex ratio near 105 at the beginning of the study period, a spike in sex ratio towards the middle of the study period, and a return to sex ratios around 103 in recent years

7.3 Results

7.3.1 Sex Ratio Trends

Figure 7.3 shows sex ratios for the Matlab population from 1966 to 2010 for four age groups: birth, 0–1, 1–4, and 5–9 (ICDDRB 1981; ICDDRB Workbook 2012). Curves are plotted using loess regression with a span of 0.25. Matlab sex ratios began at around 105 in the early years of the sample, then rose in the late 1970s and 1980s to a high near 112 for ages 5–9, then dropped close to 100 around 1990, before slowly rising again to around 103. Cohort patterns can be viewed by looking first at the sex ratios at birth and 0–1, then following the trends for sex ratio at ages 1–4 and then 5–9 a few years later. A cohort effect can be seen between the mid-1970s and early 1990s. Sex ratios at older ages (0–1, then 1–4, then 5–9) are increasingly higher, suggesting greater female than male mortality at young ages in this period. These effects disappear in the mid-1990s, replaced by relatively similar sex ratios in different age groups and cohorts.

In addition, several patterns seen in Fig. 7.3 may be related to historical events. The Bangladesh Liberation War in 1971 was attended by widespread food shortages, social unrest, and mass killings which spread from the city to village areas (Nowak 1993). During 1971–1973, sex ratios in the 0–1- and especially the 1–4-year-old cohorts increased. Shortly thereafter, a 1974–1975 flood and devastating famine may have contributed to rising sex ratios in the 0–1 and 1–4 cohorts. Peak sex ratios in the early 1980s may be related to a major shigellosis epidemic in 1984 which had strong mortality effects on children aged 0–1 and especially 1–4. After this, sex ratios gradually fell, though they rose again slightly after a 1991 cholera epidemic before leveling off.

These data suggest that high mortality events in the 1970s and 1980s may have contributed to high sex ratios through excess female child mortality. This runs counter to the costs of reproduction model, from which we would expect excess male mortality in conditions of stress. It is possible that the effects of mortality events may not have been profound enough to affect the sex ratio at birth. Moreover, the higher rates of male survival during this period suggest intentional parental protection of sons or neglect of daughters, particularly during childhood, a finding consistent with reports of son preference in Bangladesh and the region (Clark 2000; Das Gupta et al. 2003). Despite additional mortality events, the unbiased sex ratio in recent years shows smaller sex ratio perturbations, possibly due to better medical care.

For the women in our survey, Fig. 7.4 shows the average number and sex ratio of surviving children grouped according to the year each woman was 18, the median age at first birth in our sample. To smooth out sampling variation and focus attention on women who are likely to have completed fertility, we show a running average (the year the woman was 18 ± 3 years) and limit the figure to women who were 18 or older in 2000. Between 1965 and 2000, the sex ratio among surviving children declined from about 125 to 100, although fluctuations were visible. Many older women in the early part of the sample have lost children, and many of those lost children were female, consistent with a pattern of son preference in nutrition and/or medical care. By the later part of the sample, however, sex ratios became lower and more stable, likely reflecting reductions in mortality due to better medical care and reduced son preference.

The correlated declines in sex ratio and fertility in our sample contrast with the increasing male bias found in parts of India and China during fertility transition (Guilmoto 2009; Nie 2009; Sekher and Hatti 2010). Also, although a sex ratio of 100 is low by global standards, it may reflect an emerging norm that favors two children, specifically one son and one daughter (Fraser 2011). And although sex ratios have fallen at the same time as the number of surviving children, we find that when controlling for age, women with four or fewer children had significantly higher sex ratios than women with five or more children, controlling for age (Tables 7.4 and 7.5). This pattern is replicated in every 5-year cohort between 1966 and 2010.

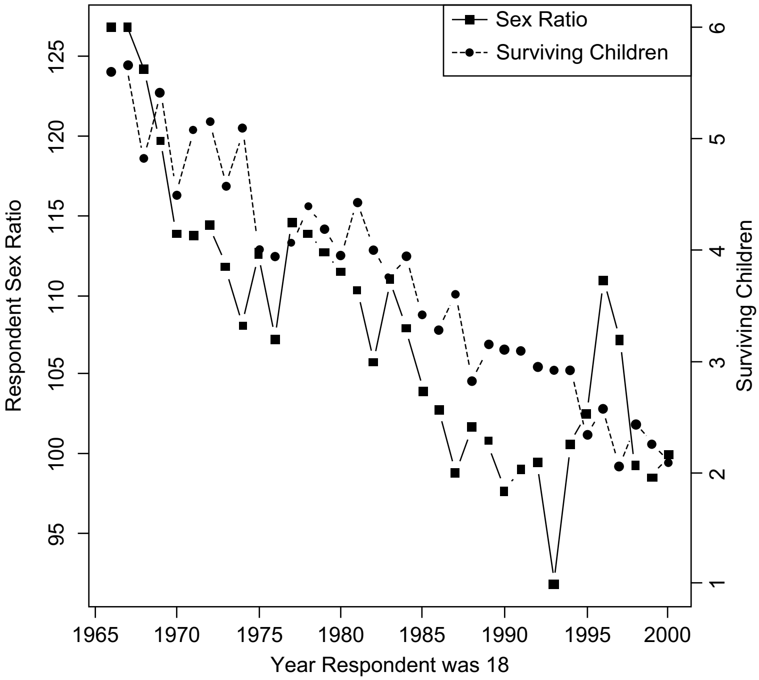

Fig. 7.4 Sample sex ratio and average number of surviving children by time. The x-axis groups women born in the same year and displays the year they were 18 years old (the average age of first birth). The left y-axis plots the sex ratio in our survey sample (*solid line*). The right y-axis plots the average number of children surviving to age 10 in our survey sample (*dashed line*). The figure suggests that sex ratios within our sample have become increasingly less male biased at the same time as fertility per woman has declined

7.3.2 Offspring Sex Ratios

Table 7.3 gives the sample sex ratios according to each predictor variable, with continuous variables turned into categorical variables for summary purposes only. Many of these cross-tabulations indicate meaningful sex ratio variation in the sample and some appear to match theoretical predictions. Table 7.4 summarizes the multi-model inference of offspring sex ratio using all variables. Of the 14 variables analyzed, a dummy variable for high fertility (five or more children), woman's age at marriage, and household income emerge as strong predictors, seen in the number of times each appears in the top 100 models, as well as their calculated importance values. The next six variables (woman's age, engagement of the family in agriculture, value of wedding gifts, woman's years of education, the husband's location, and the number of child deaths in the woman's marital *bari*) have meaningful explanatory power in at least some number of the models, while the remaining five variables (including male neonatal mortality rate, husband's education, food

Table 7.4 Multi-model inference: summary for full set of predictor variables

Variable[a]	Sign[b]	N in top 100 (no filter)	Importance ($\Delta_i \leq 6$, filtered)
Whether woman had high fertility (B)	−	100	1.00
Woman's age at marriage (B)	−	98	0.81
Household income (TW)	+	97	0.78
Whether family engaged in agriculture (LR)	+	80	0.61
Woman's age (B)	+	67	0.69
Value of woman's wedding gifts (LR)	+	66	0.38
Woman's years of education (TW)	−	62	0.42
Husband's location (TW)	+	52	0.43
Number of child deaths in marital bari (C)	+	49	0.32
Male neonatal mortality rate when woman age 18 (C)[c]		17	0.10
Husband's years of education (TW)[c]		14	<0.01
Whether woman experienced food insecurity (C)[c]		8	0
Whether family owns land (LR)[c]		4	0
Whether woman lost a child (C)[c]		3	0

[a] B=base (control) variable; TW=Trivers–Willard model; LR=Local Resource Enhancement/Competition model; C=Costs of Reproduction

[b] Refers to the sign of the variable's model coefficient, with positive values correlating with higher probability of surviving sons as the variable value increases, and vice versa

[c] Does not appear in the averaged model (Table 7.5), so no meaningful coefficient sign

insecurity, whether the family owns land, and whether the woman has lost a child) garner little to no importance among the filtered competing models.

Table 7.5 shows the averaged model resulting from our model selection and multi-model inference approach. In running diagnostics on the averaged model, we find that the predicted number of sons for each woman is strongly correlated with her actual number of sons (adjusted $R^2 = 0.463$, $p < 0.001$) with the caveat that the binomial distribution itself typically explains a large portion of the variance in sex ratio studies. All three of our control variables have significant effects on offspring sex ratio: older women have more sons, women who married at older ages have fewer sons, and women with five or more surviving children have fewer sons. Although we do not include a cohort variable, we have examined cohort effects in our analysis and they did not add any additional explanatory power. Temporal variation and secular trends are much better explained by the three control variables used here. While we use these variables as controls, they are also interesting in their own

Table 7.5 Model averaging of sex ratio predictor variables

Variable[a,b]	Estimate[c]	Adjusted SE	z value	*p* value
Intercept	–0.561	0.665	0.84	0.399
Woman's age at marriage (B)	–0.038	0.016	2.36	0.018
Woman's age (B)	0.011	0.005	2.15	0.037
Whether woman had high fertility (B)	–0.312	0.094	3.30	0.001
Household income (TW)	0.093	0.040	2.32	0.020
Husband's location (TW)	0.281	0.161	1.74	0.082
Woman's years of education (TW)	–0.023	0.014	1.69	0.092
Whether family engaged in agriculture (LR)	0.153	0.080	1.90	0.057
Value of woman's wedding gifts (LR)	0.015	0.008	1.82	0.069
Number of child deaths in marital bari (C)	0.034	0.021	1.67	0.095

[a] Variables are listed in order of model they are associated with

[b] B=base (control) variable; TW=Trivers–Willard model; LR=Local Resource Enhancement/Competition model; C=Costs of Reproduction

[c] + sign means boys more likely, – sign means girls more likely

right. Older women had offspring at a time when both fertility and sex ratios were high, likely underlying the positive association of maternal age and sex ratio. The negative relationship between sex ratio and age at marriage may be related to the fact that in the earlier years of our sample age at marriage was low and sex ratios high, while in recent years later marriage and lower sex ratios became more common. The fact that this relationship exists despite a control for age, however, is also consistent with a life history perspective, namely that women who marry later—and thus have more limited opportunities to reproduce—will be less likely to manipulate the sex ratios of their offspring. Finally, the relationship between high fertility and low sex ratios suggests that couples may either have a larger number of children in pursuit of a certain number of sons or that parents who have sons initially limit overall fertility to focus on investment in those sons.

Several variables derive from the Trivers–Willard model. As predicted, household income has a strong positive effect on offspring sex ratio, suggesting that wealthier families have more sons. The husband's labor migration abroad also has a positive effect on sex ratio, perhaps because having a son or husband working abroad is a strong index of wealth and a local status symbol. Unlike other status measures, woman's education has a negative effect on sex ratio. Controls for other variables suggest that this is not simply due to her age, age at marriage, or wealth. While the effect of woman's education is not consistent with a straightforward interpretation of the Trivers–Willard model, it is consistent with a cost–benefit approach to life history in which higher education of mothers may be associated with higher expected payoffs to investment in daughters (Kaplan and Lancaster 2000).

Families engaged in agriculture are more likely to have sons, whose labor is highly valued, consistent with the local resource enhancement model. The value of the wedding gifts given for the woman's marriage also increases with sex ratio. This variable is both a measure of her family's wealth and a metric of the importance

Table 7.6. Model comparison

	Narrow				Broad			
Model[a]	K[b]	QAIC[b]	Δ_i[b]	w_i[b]	K	QAIC	Δ_i	w_i
Base model	4	1678.9	2.8	0.13	4	1678.9	4.4	00.5
Trivers–Willard	6	1676.1	0	0.52	7	1675.8	1.3	0.24
Local resource enhancement/ competition	5	1678.6	2.5	0.15	7	1674.5	0	0.46
Costs of reproduction	5	1678.0	1.9	0.20	7	1675.8	1.3	0.24

[a] The values shown are for the model within each class that results in the lowest QAIC

[b] "K" refers to the number of fitted parameters for each model; "QAIC" refers to information criterion for the best submodel in the model class; "Δ_i" refers to the change in "QAIC" between the lowest value and the model of interest; "w_i" refers to the Akaike weight

of dowry within the study area. Higher wealth and larger dowries are predicted to bias sex ratios towards sons; thus, this finding is consistent with both the Trivers–Willard and local resource competition models. Judging which variables are better included in Trivers–Willard versus local resource models is not always obvious. Any variable attributed to local resource competition or enhancement could be an indicator for Trivers–Willard, if transmitted across generations, and any variable attributed to Trivers–Willard could be a local resource indicator, if it needed to be shared between offspring of the same sex. We return to this concern into account in Table 7.6.

Finally, one variable from the costs of reproduction model appears in Table 7.5; the other variables modeled did not have sufficient importance to be retained (see Table 7.4). The number of child deaths in the woman's marital *bari* (an indicator of levels of risk and mortality in the woman's local environment) is correlated with *more* male-biased sex ratios, not less, and thus does not support prediction 2. On the other hand, one could argue that this effect is consistent with Fisher's (1930) prediction, also discussed in costs of reproduction, that when sons are more vulnerable to mortality than daughters, they should be on average cheaper to produce, potentially leading to male-biased sex ratios. This effect is, however, quite difficult to interpret for the Matlab population. While male neonatal mortality is higher than female neonatal mortality in Matlab (ICDDRB 2012b), possibly related to greater male vulnerability, infant and childhood mortality rates are more often female biased (ICDDRB 2012b). This is consistent with reports of higher female mortality in South Asia and may indicate son-biased investment during childhood (e.g., Miller 1981). Thus, in our sample, the positive relationship between local mortality and sex ratio may be driven not by biased sex ratios at birth, but rather by higher levels of child mortality in the past when son preference norms were stronger and access to medical care much more limited.

Table 7.6 shows a model comparison of the Trivers–Willard hypothesis, the local resource enhancement/competition model, and the costs of reproduction model. Assigning predictors is complicated, however, since some predictors can plausibly belong to more than one model. Therefore, a narrower and a broader version of each model is compared—the narrower version containing only those variables most closely related to the model with overlap only in the base (control) variables, while the broader version contains a larger number of potentially related variables, some of which overlap between models. All models include the variables woman's age, age at marriage, and fertility level as controls, with a base model containing only these three variables included in the comparison.

Models are compared by beginning with a set of variables (either narrow or broad), then reducing each to its most parsimonious version. These parsimonious versions are then compared using Akaike weights. The narrow version of the costs of reproduction model includes child deaths in the marital *bari,* male neonatal mortality, whether the woman has lost a child, and food insecurity; the broad version adds household income as a measure of the woman's access to resources and thus ability to invest, the value of the woman's wedding gifts as a measure of the costs faced by daughters, and woman and husband's education as an indication of their expectations about the costs of educating daughters and sons. The narrow version of the Trivers–Willard model includes household income, husband's location, woman's education, and husband's education; the broad version adds two less direct measures of family status: whether the family owns land and the value of the woman's wedding gifts. Lastly, the narrow version of the local resource model includes family involvement in agriculture, the value of the woman's wedding gifts, and whether the family owns land; the broad version adds household income as a more general measure of the potential for competition among siblings.

The Trivers–Willard model has the highest Akaike weight and appears to be the model with the most explanatory power in the narrow model comparison, but the local resource Model comes out ahead in the broad model comparison, where broad versions of the Trivers–Willard and costs of reproduction models are exactly the same. Yet, in both cases, weight is shared among several models, suggesting that no single model has a clear advantage in terms of explaining variation in offspring sex ratios in Matlab, but rather that several types of causal explanation may be interacting. Given that this is observational rather than experimental data, it is hard to distinguish between models, and more than one model may contribute to the efficacy of a particular variable. A good example of this is the strong relationship between household income and higher sex ratios. There are many reasons why income could be so important: (a) Wealthier families/women are more able to bear the high costs of producing sons and raising them to maturity (costs of reproduction), or (b) higher-status families are more motivated to raise sons because of their potential to produce higher numbers of grandchildren (Trivers–Willard), (c) in rural areas, wealthier families are more likely to own land and need help from sons to make that land productive (local resource enhancement), or (d) that all three of these factors may be acting simultaneously.

The overall best model includes the control variables plus household income, respondent's education, husband's location, whether the family is engaged in agriculture, and the cost of gifts in the woman's marriage. This suggests that it is likely an interaction between the Trivers–Willard and local resource enhancement/competition models that may be most important in shaping offspring sex ratios in Matlab, Bangladesh. In contrast, as seen in Tables 7.4 and 7.5, most of the predictors meant to represent the costs of reproduction have very low importance and are dropped from the model, while the model that remains, child deaths in the marital *bari,* has a somewhat ambiguous interpretation. This could either mean that the model is not particularly important in the Bangladeshi context or that the variables we used to test it were not ideal.

7.4 Discussion

Child sex ratios in Matlab have declined from around 112 in the late 1980s to the current low rate of 103. A sex ratio of 112 is a bit higher than the 2011 national average for India, where sex ratios are increasing and some states have child sex ratios as high as 120. In contrast, the current Matlab sex ratio resembles regions like Kerala or Meghalaya states in India, Nepal, and Sri Lanka, which have long histories of low sex ratios. Bangladesh is therefore not just an anomaly because its current sex ratios are low but because it has recently undergone a relatively substantial *decline* in sex ratio—counter to the trends in much of the rest of the subcontinent. The national average child sex ratio for Bangladesh is 104, suggesting that our findings from Matlab are relevant to other parts of the country as well. And given its proximity to the capital city of Dhaka, Matlab is a leading rural region for other trends, such as increased labor market engagement, reduction in the agricultural workforce, and labor migration to urban areas.

Although son preference is treated by demographers as a causal variable, evolutionary demographers view it as a proximate mechanism. In Bangladesh, son preference may derive from the effects of local resource enhancement on agricultural families where sons are needed to work the land to make the family prosperous. Local resource competition between daughters related to dowry might also promote son preference, though this is unlikely to be a strong factor in Matlab, since dowry was less common during the period when Matlab sex ratios were at their highest and became more common during the past 15–20 years as sex ratios have been falling. Son preference may also result from socio-ecological circumstances that make it very important for parents to have at least one son to help earn for the family and support them in their old age.

Our results also suggest two opposing effects with respect to mortality. Male neonatal mortality rates are almost uniformly higher than female neonatal mortality rates in Matlab from 1966 to 2010, the years for which we have data (ICDDRB ICDDRB 2012b), suggesting that there is excess male mortality shortly after birth which could be related to higher costs of reproduction of sons and/or higher male vulnerability. Two pieces of evidence, however, suggest that it is excess female mortality which is the key mechanism driving higher child sex ratios in some periods. First, in 1975, during the height of one of the worst famines in recent history which produced very high rates of infant and child mortality, the male infant mortality rate was 177.0 per 1,000, while the female infant mortality rate was 203.5 per

1,000; this was during a year when the male neonatal mortality rate was 79.3 versus a female neonatal mortality rate of 76.7, suggesting that the difference occurred well after birth. In contrast, once conditions improved 2 years later, male infant mortality was 112.2, while female mortality was 113.4 (ICDDRB 2012b). Thus, in times of very high mortality, daughters suffered more than sons, while at baseline, there was little difference. Another piece of evidence comes from preliminary data on the causes of death among children in our sample. For a subsample of children for whom we could find cause of death data, there were 275 deaths among 1,205 children. The sex ratio among children who died from 0 to 1 year was 129.2, while the sex ratio among children who died from 1 to 10 was 74.6, a significant difference ($X^2 = 4.38$, $p = 0.04$, df = 1, $n = 275$). Male vulnerability could be at work in the high sex ratio among infant deaths, while the strong female bias among child deaths suggests that sons were favored in access to food or health care.

7.4.1 The Value of Evolutionary Demography

What value do evolutionary models add over other kinds of demographic models in predicting and understanding sex ratios? Our results suggest that (a) in some cases, evolutionary models produce unique predictions and predictors not found in other literature and (b) in other cases, evolutionary models yield similar predictions but tie them to a broader theoretical framework capable of yielding ultimate-level explanations. For example, the relationship between wealth and sex ratio as described in the Trivers–Willard model is not often emphasized in the non-evolutionary literature on sex ratio per se, which generally treats income/wealth as a control rather than a causal variable. Another example is the relationship between agriculture and sex ratio. Though the shift away from agriculture may be discussed in non-evolutionary approaches, predictions drawn from an evolutionary understanding of local resource enhancement do not have a direct equivalent in the non-evolutionary literature. Given that these are two of the strongest predictors of sex ratio in our model, ignoring them could lead to significant theoretical and practical oversights.

Another example of the added value of an evolutionary perspective is in the interpretation of the effect of women's education. Demographers tend to argue that women's education is a measure of female autonomy, related to women's influence on decision making, as well as an index of women's status more generally (e.g., Anderson and Eswaran 2009). An evolutionary perspective leads to a related but more precise interpretation. More educated women grew up with higher levels of parental investment themselves, suggesting an environment in which there are tangible returns to educational investment in women as well as men. Women (and their husbands) with such characteristics may perceive similar returns to investing in daughters and thus invest more equally in children of both sexes, reducing the offspring sex ratio (Hrdy and Judge 1993). Although some economic demographers (e.g., Psacharopoulos and Patrinos 2002) have examined sex-biased educational investment in terms of the marginal benefits of educating sons versus daughters, these analyses are not couched in terms of the broader, ultimate context provided by evolutionary theory.

7.4.2 Why is Bangladesh Different?

Bangladesh is culturally and economically similar to many other parts of South Asia, especially states in North India with high sex ratios. Shared cultural practices include patrilineal descent and inheritance, patrilocal residence, a strongly male-biased labor force, relatively low levels of female education, rapid economic development and urbanization, and rising dowry costs (e.g., Brooks 2012; Das Gupta and Bhat 1997; Echávarri and Ezcarra 2010; Hesketh and Xing 2006; Murthi et al. 1995; Arnold et al. 1998; Clark 2000; Das Gupta et al. 2003; Edlund 1999; Guilmoto 2009). Consequently, the low sex ratios in Bangladesh are somewhat puzzling.

There are several possible explanations for this phenomenon. It could be that shared cultural or economic circumstances are less intense in Matlab than elsewhere, i.e., incomes are lower or more equal, there is less variation in education, dowries are lower, or son preference is weaker, suggesting that the sex ratio in Bangladesh could rise with changes in these indicators. It could also be that other countervailing forces are strong enough to keep sex ratios low. Rising age at marriage, increasing women's education, and the shift away from agriculture as an occupation might be enough to counteract the effects of rising incomes and increasing international labor migration. It is also likely that wider access to medical care through ICDDRB, other nongovernmental organizations, the government of Bangladesh, and private practice have been instrumental in reducing mortality rates and thus sex ratio bias, in Matlab. Better health care has co-existed with rising sex ratios in other parts of South Asia, however, so better health care alone is unlikely to explain the low sex ratios in Matlab.

Dowry is another practice frequently cited in connection with sex ratios in South Asia. The variable gifts given at the woman's wedding show the predicted effect, though it is a somewhat a weaker predictor of sex ratio than several other variables. This may be because we are using the mother's dowry as a guide to how much parents may expect to pay for their daughters, or because adoption of the custom of dowry is relatively recent in rural Bangladesh, or because dowries are low compared to other regions, meaning that the motivation for sex ratio manipulation due to dowry remains limited. Although dowries may be higher in some parts of North India with high sex ratios, the practice of dowry is nearly ubiquitous in modern South Asia. High dowries are also found in regions without biased sex ratios, such as the state of Andhra Pradesh in India, where the 2011 sex ratio for children 0–6 was just 106.0 (Census India 2011). Alternatively, it may be that high dowries and marriage costs are not direct drivers of sex ratio decisions per se but are correlated with more relevant social features, such as rising incomes due to rapid economic development, limitations on women's work and mobility, or strong patriarchal social norms. The social correlates and consequences of dowry are complex, and several authors have critiqued the idea of a direct causal link between dowry and various kinds of discrimination against women (Shenk 2007; Van Willigen and Channa 1991).

Bangladesh also appears to be experiencing reductions in son preference. Qualitative interviews from Matlab conducted in 2010 as part of our project suggest that women now prefer one son and one daughter (Fraser 2011); it is possible that this balanced preference may be one factor driving reduced sex ratios over the past two decades. One possible source of these changing preferences is government campaigns for “one boy, one girl,” though some studies of the effects of such messages suggest their effects on behavior are limited (e.g., Shenk et al. 2013). A more convincing reason for shifting preferences may be changing socio–ecological circumstances in rural Bangladesh; as men are increasingly absent due to labor migration, daughters are filling new social roles, including caring for aging parents in the absence of a son and/or daughter-in-law. Our qualitative interviews highlighted the cultural ideal of having a son to support a family financially and a daughter to support younger siblings or aging parents physically (Fraser 2011). Similar attitudes have been found in urban Bangladesh among poor working women (Ahmed and Bould 2004), suggesting this is a social phenomenon that is not limited to rural areas.

7.4.3 Policy Implications

What will happen in the future? While increasing dowries, rising incomes, and expanding labor migration would suggest a potential future rise in sex ratios in Bangladesh, it appears that these trends are being offset by lower levels of mortality, higher women’s education, increasing age at marriage, and the shift away from agriculture. Additionally, even if many women remain housewives, our qualitative interviews suggest that men and their parents increasingly want educated, capable wives who are able to manage the family both economically and logistically in the absence of a labor migrant husband, as well as aid children (both sons and daughters) with their schoolwork. Thus, even if women are not laborers in the public sphere, the characteristics of their domestic labor may be shifting in a direction consistent with further increases in women’s education, status, and autonomy.

Some authors suggest that the lack of ultrasound technology in Bangladesh, and rural Bangladesh in particular, has kept sex ratios low (Hesketh and Xing 2006). The concern is that if such technology were to become more widely available, underlying son preferences would manifest through sex-selective abortion as has happened in many parts of India. This does not seem likely to us. Various methods of manipulating sex ratio, such as sex-selective neglect and differential birth spacing and stopping using contraceptives, are currently available to people in Matlab. Yet despite increasing access to medical technology and contraceptives in the region, sex ratios have actually declined over the past two decades, something unlikely to have happened in the face of strong underlying son preference. Moreover, many parts of South Asia which have low sex ratios (e.g., Kerala, Sri Lanka) have access to the same technologies without an increase in sex ratio. We see no indication from our data that Matlab will return to higher sex ratios simply through the availability of ultrasound technology; in fact, all indicators suggest that sex ratios will stay low —or, more clearly, balanced—well into the future.

The low, gender-balanced sex ratios in modern Matlab suggest no need for policy action at present. However, our findings do suggest which types of policies might be effective in other areas where sex ratios are high or rising. Although cause and effect are difficult to determine, policies encouraging higher female education and later ages at marriage may be effective, as might policies which lower infant and child mortality. Concern about dowry may be justified with respect to sex ratio, though given the well-known ineffectiveness (or even counterproductiveness) of laws against dowry in India, this is probably not a promising policy avenue (e.g., Shenk 2007; van Willigen and Channa 1991).

Attempting to limit rising incomes or labor migration, on the other hand, would be not only ineffective but also counterproductive to many important development goals. Despite the potential effects of rising incomes on sex ratios, the Bangladeshi situation suggests that economic growth and falling sex ratios are not incompatible. Agriculture is becoming less common as an occupation throughout South Asia, which suggests the potential for lower sex ratios. Even so, the association between agriculture and higher sex ratios suggests that policy workers would do well to concentrate efforts to reduce child mortality, encourage girl's education, and delay marriage among agricultural families.

Finally, even though public policy discussions tend to view unbalanced sex ratios as a social problem, this need not always be the case, especially if the level of bias is modest. We urge policymakers to adopt a more nuanced perspective on sex ratios and their social implications. Despite the problematic conditions for unwanted daughters, families who seek to produce a particular mix of genders in the household are usually doing so for good reasons—to keep the family economically viable, to avoid competition for resources that might lead to conflict or privation, to provide for their own support in old age, or to ensure the survival of the family or lineage. Policymakers need to balance the well-being of one family member with that of other family members; after all, it is just this kind of balancing act that parents must engage in when allocating investment within the family.

7.5 Conclusions

Our analyses demonstrate the efficacy of an evolutionary demographic approach to understanding sex ratio variation within families and regions, as well as to refining policy recommendations with respect to sex ratio. Many of our findings coincide with those of mainstream demography, yet an evolutionary approach allows us to generate new predictions as well as weave shared findings into a broader theoretical framework. We encourage demographers to consider ultimate causation when exploring issues such as sex ratio bias, and we encourage evolutionary researchers to focus beyond the traditional models of sex ratio when considering the causes of child gender preference or biased sex ratios.

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Part III
Cooperation & Conflict

Chapter 8
Evolutionary Anthropology, Co-operation and Warfare

Robert Layton

Abstract The chapter begins by reviewing recent work by Robert Kaplan and Steven Pinker, both of whom invoke Hobbes to support their argument that men are naturally violent or warlike. Kaplan and Pinker conclude that only 'strong government' can guarantee that society will not break down into anarchy. However, the failure of Western military interventions in Iraq and Afghanistan to install strong government and enforce peace points to the need for a better understanding of the dynamics of conflict and co-operation. I therefore examine critically the anthropological evidence for violence among chimpanzees and in small-scale human societies that Pinker and others cite in support of their Hobbesian arguments and identify both inaccuracies in the data cited and problems in their interpretation. In the second part of the chapter, game theory and the concept of fitness landscapes are introduced to show how evolutionary anthropology can provide a more nuanced explanation for human competition and co-operation. These provide more accurate guidelines for practical application in forestalling civil disorder or restoring peace.

8.1 Introduction

War is 'a relationship of mutual hostility between two groups where both try by armed force to secure some gain at the other's expense' (Sillitoe 1978, p. 252).

In principle, warfare can be distinguished from interpersonal violence (Younger 2008, p. 927). While the Yanomamö (Chagnon 1983, 1988) practise inter-village warfare, the Ache and Ju/'hoansi (Hill and Hurtado 1996, pp. 172–3; Lee 1979, p. 383, 389) only experience a low level of interpersonal violence, resulting in a much smaller proportion of violent deaths. Are humans naturally violent, as Thomas Hobbes (1588–1679) argued, or are they naturally sociable, as Adam Ferguson (1723–1816) countered? These apparently opposed positions have been recently restated by Kaplan (1994, 2000) and Pinker (2002, 2011) on one side and Aureli et al. (2002) on the other. How can they be resolved through a more nuanced approach that examines the conditions under which violence or peaceful sociability

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Fig. 8.1 Wola (New Guinea Highlands): a battle being fought across a sweet potato garden. (© Paul Sillitoe)

predominate, in such a way as to draw practical conclusions that can be implemented in conflict prevention and peace building?

8.1.1 The Hobbesian Position

Robert Kaplan is a US journalist who advocated the Second Iraq War and who has exercised a strong influence on the US foreign policy. In his 1994 paper ‘The coming anarchy’, Kaplan wrote:

> We are entering a bifurcated world. Part of the globe is inhabited by Hegel and Fukuyama’s Last Man, healthy, well-fed and pampered by technology. The other, larger, part is inhabited by Hobbes’s First Man, condemned to life that is ‘poor, nasty, brutish and short’ (p. 60).

Kaplan identifies the causes of Africa’s alleged descent into Hobbesian anarchy in irrational religious beliefs, loose family structure and high birth rates, declining cocoa prices, international drug cartels that have discovered the utility of weak, financially strapped West African regimes and hardwood logging that continues ‘at a madcap speed’, causing soil erosion. Beyond these specific causes, Kaplan (1994, p. 72) also finds what he calls an innate atavism: ‘In places where the Western Enlightenment has not penetrated and where there has always been mass poverty, people find liberation in violence.’

Kaplan republished this essay in a collection of the same title (Kaplan 2000). While his other essays are not always as sensationalist, the book does provide

Fig. 8.2 Wola man with a bark shield drawing his bow. (© Paul Sillitoe)

an extended argument for 'strong government'. It is prefaced with a quote from *Leviathan*, (Hobbes 1970 [1615]) 'Before the names of Just and Unjust can have place, there must be some coercive power'. The theme of man's natural propensity for violence continues: When standing armies are reduced in peacetime, 'we will have as much violence as before, only it won't take an organised form' (p. 175). Kaplan (2000, p. 178) concludes 'consensus can be the handmaiden of evil, since the ability to confront evil means the willingness to act boldly and ruthlessly and without consensus, the attributes that executive, national leadership has in far more abundance than any international organisation'.

Steven Pinker's book *The Blank Slate* (2002) is a far more substantial study than Kaplan's. Pinker is an evolutionary psychologist. His book is directed against social scientists who argue that the human mind is entirely shaped by culture. Pinker wrongly identifies Durkheim as the founding father of this argument, a point to which I will return. He introduces his case by contending that human behaviour is generated by both genes and culture but, as his argument proceeds, Pinker turns increasingly to argue that emotions and drives, in particular the propensity to violence, 'have a common logic across cultures, are difficult to erase or redesign from scratch [and] were shaped by natural selection acting over the course of human evolution' (Pinker 2002, p. 73).

Pinker begins by posing a rhetorical question: Was Rousseau (CF Rousseau [1963/1755], p. 187) correct to portray man in his natural state as a gentle creature or was Hobbes correct to argue that man's natural state was a war of every man against every other man? If Hobbes was right, then we need the police and army to enforce an 'uneasy truce', and if people are naturally nasty, then children must be disciplined and tamed (2002, p. 7). In the past two decades, Pinker contends, anthropologists have gathered data on life and death in pre-state societies, and found Hobbes was right, Rousseau wrong. Pinker's main sources appear to be Chagnon's study of the Yanomamö and two surveys by Daly and Wilson (1988) and Keeley (1996).

Pinker cites Locke and others as sources of the economic, or social contract tradition that society is an arrangement negotiated by rational, self-interested individuals. He rightly argues this theory consistent with 'the modern theory of evolution'; reciprocal altruism is the social contract restated in biological terms (2002, p. 285). Behavioural strategies evolved to benefit the individual, not the community. However, he goes on to assert, as if this were a conflicting argument, that morality was preceded by billions of years of the morally indifferent process known as natural selection (Pinker 2002, p. 318). In Pinker's view, Hobbes captured 'the consequences of this background amorality…. He showed how the dynamics of violence fall out of interactions among rational and self-interested agents' (p. 318). But Hobbes also showed us the solution, 'a governing body that is granted a monopoly on the legitimate use of violence can neutralise each of Hobbes' reasons for quarrel…. Adjudication by an armed authority appears to be the most effective violence-reduction technique ever invented' (Pinker 2002, p. 330). Just to make it clear that he is recommending a policy of autocratic authority, Pinker adds: 'Democratic leviathans have proved to be an effective anti-violence measure, but they leave much to be desired' (p. 332).

In Pinker's more recent book *The Better Angels of Our Nature* (2011), Hobbes remains a qualified authority. Hobbes 'used fewer than a hundred words to lay out an analysis of the incentives for violence that are as good as any today' (Pinker 2011, p. 33). Hobbes was describing a state of anarchy, and 'Archaeologists tell us that humans lived in a state of anarchy until the emergence of civilisation some five thousand years ago, when sedentary farmers first coalesced into cities and states' (p. 35). On the other hand, Pinker now concedes that Hobbes 'got a lot of it wrong' (p. 52) and democratic leviathans are given more credit.

Considering the slender character of Hobbes's argument, and the existence of competing theories of human nature in seventeenth-century political philosophy, it is surprising that Hobbes can still be cited as an authority. Hobbes's method was to start from the essential properties of the natural kind or class of things—such as *man*—and derive a universal principle:

> By experience known to all men and denied by none, to wit, that the dispositions of men are naturally such that except they be restrained through fear of some coercive power, every man will distrust and dread each other. (From *Philosophical Rudiments,* quoted in Peters 1967, p. 62)

Hobbes was not, then, the kind of academic authority such as Darwin, whose conclusions are based on extensive empirical research, but rather the sort that has derived axioms from first principles. The salience of Hobbes's book *Leviathan* stems partly from the moment that it was published, shortly after the English Civil War. During the period between the King's execution in 1649 and Cromwell's assumption as Lord Protector in 1653, 'there was constant discussion and experimentation to find an appropriate form of government to succeed the monarchy' (Peters 1967, p. 31). Hobbes's arguments were therefore used both to justify Cromwell's Protectorate and the restoration of Charles II. 'The doctrine of sovereignty which emerged from his writing was one that could be used to justify any absolute *de facto* government' (Peters 1967, p. 32).

I will argue that a more nuanced understanding of human violence can be gained by taking an 'ecological' approach to social relations, according to which there may be certain social circumstances that encourage violent competition for desirable resources and other circumstances that favour peaceful co-operation. The conditions conducive to peace or violence are addressed with regard to Polynesian islanders by Younger (2008). Younger uses statistical methods, identifying population size, degree of isolation and egalitarianism or hierarchy as key variables contributing to a peaceful or violent society, but I will take a more dynamic approach to explain the evolution of social strategies in different natural and social environments. When writers are reluctant to acknowledge such more complex scenarios, they must bolster their selective use of empirical evidence by appealing to the axiomatic truths put forward by an authority. This may particularly be the case where the writer's own interest group has been instrumental in constructing an adverse social environment for others, or where he seeks justification for authoritarian government.

8.2 Competing Arguments

Hobbes was not the only political theorist stimulated by the English Civil War. The Levellers were a radical political sect active during the Civil War, who campaigned against the monarchy and private property, and in favour of universal male suffrage. While they fought on the Parliamentary side in the Civil War, they were not popular with Cromwell, who had some of them executed. The Levellers were among the political thinkers of the Enlightenment who had been inspired by Tacitus's account, in Chap. 11 of his *Germania*, (Tacitus 1985) of the rough-hewn democracy of the Germanic peoples beyond the edge of the Roman Empire. *Germania* was republished in Antwerp in 1574 (Dudley 1968, p. 234). Its rediscovery had a profound effect on English political thought, as Tacitus's Germanic people were taken to be the ancestors of the Anglo-Saxons. Tacitus's account stimulated the political theory of the 'Norman Yoke', that the Norman Conquest had imposed an oppressive, centralised hierarchy on what had been a more egalitarian Anglo-Saxon society that brought the principles of Germanic democracy to England (Hill 1958). The broadest interpretation made by seventeenth-century writers was to equate the Anglo-Saxon society with the natural human state of primitive communalism. Hill argues that the Levellers were the first to deduce from this a universal principle, the natural rights of man (Hill 1958, p. 81).

8.2.1 John Locke

Another possibility—championed by John Locke and Adam Ferguson—is that humans have always been capable of building co-operation and reciprocity because they recognise that social order is in their long-term self-interest. Locke published his *Two Treatises of Government* in 1689, 30 years after Cromwell's death. Locke argued that people possessed 'natural rights' that they were entitled to defend against an oppressive state. 'Men living together according to reason, without a common Superior on Earth with Authority to judge between them, is *properly the state of nature*' (Locke [1960/1689], p. 280, his emphasis).

Locke's approach was taken up in the following century by Adam Ferguson, who wrote 'Mankind are to be taken in groupes [sic], as they have always subsisted' (Ferguson [1995/1767], p. 10). Before the state assumed responsibility for upholding the law, people owed their safety to 'the warm attachment of their friends, and to the exercise of every talent which could render them respected, feared or beloved' (p. 211). They were 'intangled [sic] together by the reciprocal ties of dependence and protection…' (p. 71). Ferguson may have been thinking of the Levellers' argument for the origin of democracy in ancient Germanic society when he wrote, 'The inhabitants of a village in some primitive age, may have safely been intrusted to the conduct of reason to regulate their own affairs' (Ferguson 1995, p. 63), but he also had access to the account of the Iroquois Confederacy published by the French missionary and anthropologist Lafitau (1681–1746), a social order which, Ferguson concluded, was rationally sustained by its members' self-interest (Ferguson 1995, p. 64).

A recent restatement of this view has been put forward by the primatologist Felipo Aureli and colleagues. Aureli et al. (2002, p. 325), writing generally about primates (apes and monkeys), point out that 'for gregarious animals, conflict of interest, while unavoidable, may compromise the benefits of group living or neighbourliness, *especially when it escalates into aggression*' (my emphasis). Male chimpanzees within a community engage in reconciliations after conflict more frequently than do females (Aureli et al. 2002, p. 334).

8.3 The Evidence for Levels of Warfare in Stateless Societies

To disentangle the levels of inaccuracy and misunderstanding perpetuated by Kaplan and Pinker, we need first to look at the evidence on which they rely, and second at how it is misrepresented. Proponents of the argument that mankind's innate violence constantly threatens to undermine society find Chagnon's study of the Yanomamö a particularly useful source, and Pinker cites him repeatedly. I therefore start this section of the chapter by looking critically at Chagnon's data, and at the use made of these data by Wrangham and Peterson in their 1997 book *Demonic Males: Apes and the Origin of Human Violence.* It should be noted that while they provide information that would support a Hobbesian argument, neither Chagnon nor Wrangham and Peterson explicitly cite Hobbes. Their argument with regard to forms of government is simply that a centralised state can guarantee a lower level of violence than exists among stateless societies. Chagnon (1988, p. 990) cites the case of a young Yanomamö man who went to the territorial capital to be trained as a nurse, where he discovered police and laws. He told Chagnon how he had visited the territorial governor and urged him to make both police and law available to the Yanomamö. Wrangham and Peterson (1997, p. 77) propose that to combat men's genetic capacity for violence, people have built civilisations with laws and justice, diplomacy and mediation (Wrangham and Peterson 1997, p. 198).

8.3.1 Chagnon on the Yanomamö

The Yanomamö, horticulturalists (swidden cultivators) in forests on the borders of Venezuela and Brazil, live in semi-permanent villages. Chagnon treats each Yanomamö village (correctly) as a 'sovereign' entity. Alliances are based on the regular exchange of women in marriage (Chagnon 1983. p. 149). No village can continue to exist as a sovereign entity without establishing alliances with other groups (p. 147). Despite an agreed gradation in levels of violence, including chest pounding and club fights (p. 66), which enables people to resolve grievances without killing (p. 170), warfare is endemic among the Yanomamö, and accompanied by a 'bellicose' ideology that strong villages should take advantage of weaker ones by capturing their women. Chagnon argues (1983, p. 86) that the desire for women causes 'much' of Yanomamö warfare; but later he writes, 'Although few raids are initiated solely with the intention of capturing women, this is always a desired side benefit' (p. 175).

In his 1988 paper, Chagnon claimed that violence enhances male reproductive success; men who have killed more people have more wives and children than men who have not killed. Such men are called *unokai.* Chagnon (1988, p. 985) does not claim the existence of a gene/allele for violence, but he does claim that being a killer among the Yanomamö enhances one's reproductive success. Warfare is therefore adaptive (for men!) among the Yanomamö, and the Yanomamö are typical of 'primitive societies' (1988, p. 985). This is echoed by Pinker, who comments that such arithmetic, if it persisted over many generations, would favour a genetic tendency to be willing and able to kill (2011, p. 612).

Chagnon has probably inflated the proportion of genuine 'killers' in the population. His 1988 paper records that 44 % of men over 25 claim to have killed someone, but only 30 % of adult men died violently (Chagnon 1988, p. 987 versus p. 986). Seventy-five percent of claimed killings (p. 262, 345) can be accounted for by the 54 *unokai* who reported having killed two or more men (Chagnon 1988, Fig. 1, 'Number of victims for which living killers *unokaied*'). These 54 constitute a mere 14 % of the adult male population of 380 included in Chagnon's Table 3 ('Marital success of *unokais* and *non-unokais*'). Chagnon has demonstrably exaggerated *unokais'* relative reproductive success by adding up the number of children born to *unokai* and non-*unokai* of all ages above 20 and concluding that *unokai* have three children for every one born to a non-*unokai*. Many non-*unokai* are young men just starting to have children. Their family size will inevitably be smaller. Survivors may claim *unokai* status later in life. The most accurate measure of the advantage of being an *unokai* is to compare reproductive success among *unokai* and non-*unokai* over 40, where family size is most probably complete. *Unokai* over 40 have 1.67 children for every child born to a non-*unokai*. They are advantaged, but not to the extent implied by Chagnon's all-age ratio of 3:1.

8.3.2 Wrangham and Peterson: Demonic Males

Wrangham and Peterson, whom Pinker (2002) also cites, go further than Chagnon in three respects. First, they equate the Yanomamö with the original human condition. While admitting that the Yanomamö are not hunter-gatherers they contend that 'No human society offers a better comparison in this regard [with chimpanzees]… because they have been so remarkably protected from modern human influences' (1997, p. 64). Wrangham and Peterson blithely disregard the fact that, far from 'uncontaminated' by contact with the outside world, the Yanomamö have interacted with outsiders since the eighteenth century, as victims of slave raiders, enemies of settlers and subjects of missionary endeavours (Fischer 2001).

Second, they argue explicitly for a genetic basis to human violence (1997, p. 196, 198). Has sexual selection shaped our psyches, to make us better fighters? they ask rhetorically (p. 182). Is it the emotion of pride that underlies violence among both chimpanzees and humans (p. 190)? The road from 'maybe' to 'is' is short one, and two pages later they conclude that 'the molecular chemistry of DNA…contains destructive elements' (Wrangham and Peterson 1997, p. 198). This conclusion allows Wrangham and Peterson to go further than Chagnon in a third respect, tracing the origin of human violence to our primate ancestors prior to the divergence of the evolutionary pathways leading to modern humans and chimpanzees (i.e. a period of more than 6 million years), an argument paraphrased by Pinker (2011, p. 38).

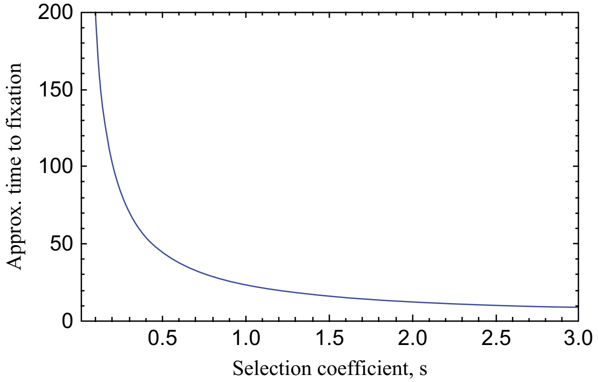

Fig. 8.3 Graph showing the number of generations required (*vertical axis*) for a fitter allele to displace a less fit, alternative allele, depending upon the fitness differential between the two alleles (*horizontal axis*)

Chimpanzees, Wrangham and Peterson write, provide 'surprisingly excellent models of our direct ancestors. It suggests that chimpanzee violence preceded and paved the way for human war' (p. 63). 'Our ape ancestors have passed to us a legacy… written in the molecular chemistry of DNA' (p. 198) which causes our desire to intimidate the opposition.

For Yanomamö *unokai* over 40 to have 1.67 children for every 1 child born to non-*unokai* in the same age bracket is, in terms of Darwinian natural selection, a huge advantage. Suppose we interpret Wrangham and Peterson's (1997, p. 198) claim that human violence is 'written in the molecular chemistry of [our] DNA' at its most literal, and postulate a model in which there were two alleles of a gene, one causing a peaceable character in men and the other a violent disposition. If those men carrying the violent allele have 1.67 children born for every 1 child fathered by a man carrying the allele for a peaceable nature, the 'violent' allele would quickly displace its alternative in a population of similar size to the Yanomamö. In an effective population of approximately 500, a single allele with a biologically plausible yet still large selective advantage of 1.1:1.0 over another at the same locus, with no dominance assumed, can spread within approximately 190 generations, or 5,000–6,000 years (see Fig. 8.3).[1] If the reality were as simple as this, then the present state of affairs among the Yanomamö would be transient and certainly not the original human condition. Approximately 38 % of Yanomamö men aged 41 or over in Chagnon's sample claim *not* to be *unokoi;* so, if such a selective process is at work, it is still incomplete. Further, Chagnon only documents the situation

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[1] Ewans's (2004) equation 1.28, $t(x_1,x_2)=\int_{x_1}^{x_2}\{1/2Sx(1-x)\}^{-1}\,dx$, gives the time required for the frequency of an allele to move between two values x_1 and x_2, assuming the fitness differential, s, in a bi-allelic system and in the absence of any allelic dominance. The following graph shows the time taken (in generations) for the allele to spread from its initial frequency $x_1=1/N$ through to $x_2=1-4(2Ns)^{-1}$ (see Ewans, Eq. 5.50), which is close to fixation (assuming high s) and beyond which dynamics are stochastic.

over two generations. It is possible that non-*unokai* have more surviving grandchildren than do *unokai*.

How valid is Wrangham and Peterson's claim of violence among chimpanzees? Both Goodall (1986) and Nishida et al. (1985) reported cases of chimpanzees (*Pan troglodytes*) extending their territories by attacks on adjacent groups, apparently supporting the claim of a direct connection between male chimpanzee aggression and human warfare. Among both chimpanzees and many small-scale human societies, it is females/women that leave their natal group to join the group in which they will reproduce. The discovery that females also move between groups among chimpanzees potentially throws light on the origin of the intergroup alliances in human society (Rodseth et al. 1991) and provides grounds for contending other groups were attacked to obtain their women rather than their territory (e.g. Chagnon 1997, p. 97).

There is, however, still some question as to how typical is the pattern reported by Goodall, and to what extent it may have been influenced by the research team's practice of supplying the Gombe chimpanzees with bananas. After the supply of bananas had been drastically reduced, the Gombe community split into two groups and became polarised within a range they had previously apparently shared. Over a period of 2 years, the males of the larger group killed at least some of those in the smaller group, and took over their territory. Encroaching farmers may also have displaced other chimpanzees into the area, increasing the pressure on food resources (Ghiglieri 1984, p. 8). The Mahale Mountains of Tanzania, on the eastern side of Lake Tanganyika, contain at least eight chimpanzee communities (Nishida et al. 1990, p. 66, Table 3.2). While territories are generally exclusive, groups 'M' and 'N' showed, for a time, some overlap of ranges (Nishida et al. 1990, p. 71, Fig. 3.4). Group 'M' subsequently gained exclusive access to the area previously shared. There is circumstantial evidence for raiding, but no direct evidence that one group of males systematically wiped out another in order to gain access to females. While the killing of vulnerable individuals in border zones is now well documented (Wilson and Wrangham 2003; Wilson et al. 2004), Manson and Wrangham (1991) acknowledged that there are only two known cases (one confirmed and one probable) of group extinction via lethal raiding (Manson and Wrangham 1991, p. 371; Wilson and Wrangham 2003, p. 372). Sean O'Hara (personal communication), who carried out field research at Budongo where there was less pressure on land, found that male chimpanzees there engaged less frequently in border patrols (see Reynolds 2005; Bates and Byrne 2009), further questioning the universal applicability of the Gombe incident.

Mameli and Bateson (2006) discuss 26 possible scientific definitions of innateness. Among these 26, they identify 8 that are reasonably sound and test each against 9 case studies of behaviour for which claims of innateness have been made. The three that score most highly are (see their Table 1, p. 177 and Table 2, p. 180):

- Definition 3: 'It reliably appears during a particular stage of the life cycle', e.g. onset of sexual maturity—but, they note, this can also be characteristic of learned traits (p. 158).

- Definition 12: ‘All environmental manipulations capable producing an alternative trait are evolutionarily abnormal’ (p. 164).
- Definition 25: ‘It is a standard Darwinian adaptation’—but they note again that many learned traits are standard Darwinian adaptations, albeit transmitted by culture (pp. 173–4).

In the following paragraphs, I will argue that none of these three definitions justify treating human aggression as an innate trait.

8.3.3 The Evidence from Hunter-Gatherers

Wrangham and Peterson are surprisingly vague about violent combat among hunter-gatherers. ‘Unfortunately for anthropology, much less is known about warfare among equivalently isolated foraging people’ (Wrangham and Peterson 1997, p. 71), but they seek to dispel the notion that hunter-gatherers are peaceful, citing a survey of 31 hunter-gatherer societies by Ember (1978) which reported that 64 % engaged in warfare once every 2 years (p. 75). They also cite Eibl-Eibesfeldt (1989), another secondary source, for the statement that among the ‘Murngin’ (Yolngu) of northern Australia, 28 % of deaths were due to warfare (Wrangham and Peterson 1997, pp. 75–77), but Eibl-Eibesfeldt has misquoted his primary source, Lloyd Warner. Warner, who conducted extended fieldwork among the Yolngu from 1926 to 1929, estimated that in a population of around 1,500 men, approximately 200 had been killed over a period of 20 years (Warner 1958, p. 147), and not 200 out of 700, as reported by Eibl-Eibesfeldt. This gives a substantially lower proportion of violent deaths at c. 13 %.

Pinker’s Fig. 2.2 (2011, p. 49) compiles ethnographic data from hunter-gatherers and hunter-horticulturalists based on secondary sources. These data include a very high figure for Ache of c. 32 % (higher than both Yanomamö samples in the horticulturalists) and far higher than Hill and Hurtado’s primary data cited below. The Murngin are still shown at c. 22 %. The table is selective, on the grounds that small bands such as the!Kung San and the Inuit ‘are not a representative sample of our anarchic ancestors’: These people, he argues, have survived as hunter-gatherers only because they inhabit remote parts of the globe that no one else wants (Pinker 2011, p. 41), and the environment of evolutionary adaptedness ‘is not the cut that is most relevant to the Leviathan hypothesis’. Pinker asserts that the inhabitants of ‘flusher environments’ such as the Northwest Coast of North America, Amazonia and New Guinea, although they practise swidden cultivation, are far closer to pure hunter-gatherers than they are to sedentary, full-time farmers (also 2011, p. 41). The Northwest Coast and Amazonian cases will be re-examined below.

Primary data are given for the Ache of Paraguay by Hill and Hurtado (1996) and for the Ju/’hoansi (!Kung) of the Kalahari by Lee (1979). Hill and Hurtado (1996, p. 172–3) calculate the proportion of total deaths attributed to violence, among all individuals aged 15+, when the Ache lived as hunter-gatherers before settlement on a mission (Table 8.1).

Table 8.1 Causes of death among Ache hunter-gatherers. (Hill and Hurtado 1996, p. 172–3)

	Male	All (male + female)
Total deaths:		
of which caused by violence:	103	153
Abandoned	2	5
Club fight/killed by Ache	9	11
Shot by Paraguayan	33	48
Captured by Paraguayan	0	1
Subtotal	44	65
Percentage of deaths due to violence		
Between Ache	11 %	10 %
From Paraguayans	32 %	32 %

Table 8.2 Causes of death among Ju/'hoansi hunter-gatherers. (Lee 1979, p. 383, 389)

In the course of feuds	15
Single killings that did not provoke retaliation	7
Marital disputes	5 (including 2 women)
Innocent bystanders	At least 5 (including 1 woman)

Lee (1979, p. 383, 389) identified 32 instances of homicide among Dobe Ju/'hoansi during the 35 years between 1920 and 1955. These are listed in Table 8.2.

In 1964, the Ju/'hoansi population at Dobe, including temporary residents was 466, while in 1968 it was 584 (Lee 1979, p. 43). A total of 32 deaths in a population of approximately 525 is equivalent to 6 % of the population dying violently over 35 years. These data show that violent death may be much less prevalent among hunter-gatherers than among the Yanomamö, and also lower than implied by Pinker's data (Pinker 2011, p. 54 argues the!Kung were more violent during the time they fought encroaching Bantu pastoralists and European settlers).

Warfare among hunter-gatherers is not always as ruthless as Pinker reports. In 1932, the Australian anthropologist Stanner witnessed a 'large-scale fight' between two Aboriginal groups. Despite the 'anger, challenge and derision' on both sides, there was also control. Only light duelling spears were in use. Towards sunset, the battle ceased 'and some of the antagonists began to fraternise'. Several weeks later, Stanner attended an initiation ceremony. Both sides to the dispute were present. Even though they were 'at violent enmity…. The bad feeling had been suppressed, after the aboriginal fashion, for a necessary tribal affair' (Stanner 1960, p. 65–7).

It is true that warfare was endemic among hunter-gatherers on the Northwest Coast of North America in the recent past, but the origin of this intensive warfare can be estimated from the archaeological record. The Northwest Coast has been inhabited by hunter-gatherers since 9000 BC (Maschner 1997). During the long period between 9000 and 3500 BC, groups were small and mobile. The first evidence for conflict on the Northwest Coast occurs by 3000 BC, coinciding with the earliest shell middens, and is seen primarily in nonlethal skeletal injuries. This was probably due to stabilisation of the postglacial sea level; a denser and more predictable resource distribution allows stronger territoriality (Maschner p. 210 ff, 217). In the ‘Middle Pacific’ period (1800 BC–AD 200/500), skeletons from northern areas evidence a sharp upsurge in hand-to-hand fighting, with 48 % showing some injury, although only 15 % of skeletons from further south show such injuries. From AD 200–500, however, the onset of warfare is evident in the construction of defensive sites, the aggregation of what may have been single lineages into large community villages and population decline. The bow and arrow were introduced to the region at that time, intensifying the violence of conflict. Northwest Coast warfare is a product of specific ecological and social conditions.

8.4 Explaining the Incidence of Violence in Human Societies

The above evidence does not prove that hunter-gatherers are peaceful and horticulturalists warlike, but it does show that levels of violence among politically uncentralised societies vary. If we are to understand the phenomenon of violence in the absence of a sovereign, this variation is as important as its mere presence to some degree. The incidence of violence can usefully be explained by recourse to game theory.

8.4.1 Game Theory

The modern theory for the evolution of co-operation originated in John Von Neumann and Oskar Morgenstern’s *Theory of Games* (1944). The best-developed part of their theory concerned ‘zero-sum two-person games’. In a zero-sum game, the winnings are fixed, and the two players are therefore in competition to see who can gain the largest share, a Hobbesian situation. The model was taken up by post-World War II military strategists. Air battles were represented as duels between a pair of opposing planes. There was a trade-off between two conflicting strategies: waiting until the opponent approached, so as to have a better chance of hitting him, and firing first to avoid being hit: a version of the game of ‘Chicken’.

As nuclear weapons grew more destructive, however, strategists in the USA came to appreciate that the duel model was inappropriate and co-operation advantageous. The USA and the Soviet Union now shared an interest in avoiding mutually assured destruction (MAD). This dilemma posed sociologically more interesting questions. Co-operation, negotiation and disarmament could benefit both, if the other could be trusted (Nasar 1998). Was it possible to turn confrontation between the USA and the USSR. into a non-zero-sum game, without the intervention of an overarching sovereign?

The model of the *Prisoner’s Dilemma* was devised to explore how mutual trust could be achieved without the intervention of an umpire. This uses the model of two suspects who have been arrested and are being interrogated in different rooms, to explore the conditions under which co-operation can evolve. The prisoner wonders whether he can trust the other to remain silent. Each is told that, if they alone implicate the other in the crime, they will be rewarded. If both confess, both will receive a moderate sentence, since their confession helped the police solve the crime. If one refuses to confess (i.e. refuses to ‘defect’), even though the other has done so, his sentence will be heavier. If the other prisoner is suspected of having confessed, it will therefore be better to take the same course oneself (Trivers 1985, pp. 389–90).

At first sight, the most rational plan seems to be to defect rather than trust the other prisoner to remain silent (or, in the case of nuclear war, trust them to refrain from launching an attack). Mutual defection (attack) is however more costly than co-operating with the other prisoner to remain silent. Each prisoner faces the dilemma that, although defection is less risky than co-operation, if both defect they will both do worse than if they had co-operated with each other, since they would be freed if neither confesses.

The dilemma shows that if each prisoner pursues their immediate private interest every time they are arrested they do not achieve the best long-term outcome for themselves, let alone for the other prisoner; a Hobbesian war of each against all would be the result. Robert Axelrod realized that co-operation would only develop if the prisoners can anticipate each other’s intentions (Axelrod 1990). Since they are secluded from one another in the cells, anticipation must be based on prior knowledge. If the game is played once with an unfamiliar ‘partner’, the stable strategy will be to defect (Axelrod 1990, p. 10), but if it is played repeatedly by the same players the stable strategy may be to co-operate through remaining silent. To rely on co-operation, the prisoners must have already interacted with each other in ways that test their loyalty to one another. They must, in other words, have evidence of the other’s commitment to reciprocal altruism. This provided a clear explanation for the desire to perpetuate social relationships out of self-interest, the condition envisaged by Locke, by reassuring others of one’s friendly intent. The discovery led to the introduction of the original telephone ‘hot line’ directly linking the presidents of the USA and USSR.

A more sophisticated theory for the evolution of war is therefore required. The notion of warfare being hard-wired in the human genome goes against the fundamental axiom of Darwinian evolution that no adaptation is universally ‘better’ than another; each adaptation is a response to its local ecological context. Genes, individuals and species interact, each shaping the others’ *fitness landscape*.

The ‘fitness landscape’ is a model used in the Neo-Darwinian theory of evolution to represent the variable effects of natural selection on a biological population. It can be borrowed to represent the social environment in which human actors adopt particular learned social strategies (see Kauffman 1993, pp.33–36 for a summary of the ways in which biologists have used the metaphor). In a more or less uneven landscape, peaks represent effective adaptations (Wright 1932, Fig. 2). Populations climb peaks in the landscape as their members become increasingly well adapted to a particular ecological niche. However, the reproductive success of each species is partly determined by the fitness of other species such as predators, prey and symbiotic relationships with other species. The evolution of other species can thus change the shape of the landscape and destabilise existing adaptations. 'In co-evolutionary processes, the fitness of one organism or species depends upon the characteristics of the other organisms or species with which it interacts, while all simultaneously adapt and change' (Kauffman 1993, p. 33).

In an interconnected social world, the 'fitness' of local social strategies is similarly determined by interaction with other players within and between communities. Nelson and Winter (1982) introduced this approach to the social sciences in their book *An evolutionary theory of economic change*. Natural selection proceeds blindly. The extent to which human social strategies are pursued intentionally is an open question. Subsequent writers (e.g. Elster 1983, pp. 51–61; Allen 1997, pp. 43–4) tended to agree with Nelson and Winter (1982, p. 15, 276) that people are only partially informed about the outcomes of their strategies or social decisions. Intentional choice may speed up the rate at which more efficient strategies are adopted, but ultimately it is the consequences of people's choices that determine the viability of their strategies, not the actor's intentions (see discussion in Layton 2006, pp. 82–85). An extensive literature on the application of games theory has now developed in the social sciences. For the purposes of this chapter, I simply wish to point out that there are local optima in a social fitness landscape in which either co-operation or intergroup aggression may provide the most adaptive strategy, but these are shaped by ecology, subsistence strategy and intergroup interaction. In the following paragraphs, I first look at how social strategies can be modelled via game theory, and then at how local optima may lead to peace or war.

By simulating the Prisoner's Dilemma game in a computer tournament, Axelrod (1990, p. 42) found that the most stable strategy proved to be one called 'tit-for-tat', in which the player begins by anticipating the other will co-operate (and not confess) and then, in subsequent moves, does what the other player did in their previous move. In this way, other players who co-operate are rewarded, but those who defect are punished. The cumulative benefits of co-operation are greater than those of always confessing to the jailer, since mutual betrayal eliminates the reward for confession.

The point of the Prisoner's Dilemma is to show how a zero-sum game can be *transformed into a non-zero-sum game* through repeated interaction building mutual trust, *without an umpire* or sovereign, providing there is a benefit to co-operation and the opportunity to build mutual trust through repeated interaction. The Prisoner's Dilemma explains how co-operation can evolve in a 'state of nature', even when it is in competition with selfishness.

The evolutionary biologist John Maynard Smith demonstrated the usefulness of game theory in evolutionary biology in his book *Evolution and the theory of games* (1982), where he analysed, among other things, the defence of territories. Maynard Smith termed the strategy that wins against itself and all other existing strategies being played in that field of interaction an evolutionarily stable strategy (Maynard Smith 1982, p. 10), but he went on to show that strategies may be evolutionarily stable in one environment, yet not in another. This discovery makes it possible to explain why horticulturalists may behave more aggressively than hunter-gatherers (see Fig. 8.1 and 8.2).

Hunter-gatherer societies give many examples of the benefit of inter-band co-operation and the creation of opportunity to build mutual trust through repeated interaction. Most recent hunter-gatherers do not defend band/clan boundaries because defence is impracticable, nor are bands (unlike chimpanzee communities) typically patrilocal (see Hill et al. 2011; Layton et al. 2012; both of which note further objections to drawing direct parallels between the chimpanzee community and hunter-gatherer band). Peterson and Long calculate that, even in the rich tropical woodland of northern Australia when the Yolgnu ('Murngin') live, an Aboriginal band of 40 occupying a territory of 400 km^2 would have had to defend a boundary of 70 km, equivalent to 2 km for every man, woman and child. Boundary defence is therefore not practised anywhere in Australia (Peterson and Long 1986, p. 29). On the contrary, people depend on good relations with neighbouring groups, as an insurance against climatic fluctuations (drought, flood, etc.) which make it advantageous to be able to camp with another band. These relations are maintained through regular visits, meetings at collective ceremonies and classificatory kinship allowing one to treat non-kin as if they were relatives. The Ju/'hoansi have an exchange system called hxaro, which maintains an extensive network of friendships between women in different bands (Wiessner 1982). When hxaro partners live far apart, it is important to keep up a balanced flow of gifts to let each partner know the other still values the relationship. Women make long journeys to visit their partners and choose them strategically to ensure partners belong to bands located in different ecological zones.

Horticultural societies, on the other hand, are particularly vulnerable to warfare because they live in economically self-sufficient settled communities next to dense patches of desirable resources (their garden crops), but lack an overarching social organisation to regulate inter-village relations peacefully. A precarious form of reciprocal altruism is therefore negotiated around marriage exchanges that seek to guarantee order. But this order is repeatedly undermined by free riders who organise raids or split large lineages to their personal advantage, while jeopardizing the lives of others. Villages that split become enemies (Chagnon 1988, p. 987, 988). Small villages are more vulnerable to attack than large ones (Chagnon 1988, p. 986).

Helbling, who also carried out fieldwork in lowland South America, argued that the Yanomamö are trapped in a form of the Prisoner's Dilemma that discourages the development of reciprocal altruism. Each lineage must convey the impression that they are 'tough guys' rather than trusting suckers. Further, if their partners in an exchange relationship betray them, the effect of military defeat would be so devastating that it would be too late to punish the partners by not reciprocating in the next round of the game as many of the 'suckers' would be dead (Helbling 1999, pp. 108–9). This creates a social environment that favours aggressive individuals. For Pinker (2002), this is all too often the outcome of the game.

8.5 Where did Kaplan and Pinker go Wrong?

8.5.1 Kaplan

In Kaplan's image of the future world, the Last Man, healthy, well fed and pampered by technology, lives in a cocoon, insulated from the other, larger, part of the world inhabited by Hobbes's First Man. In Kaplan's opinion overpopulation, the spread of disease, deforestation and soil erosion are entirely brought about by local mismanagement. Duffield (2001, p. 27) traces the origin of the approach advocated by Kaplan to a 1981 UN report prepared by Sadruddin Aga Khan that shifted blame from the West to the victims of global change. Cocoa and hardwood timber prices do not rise or fall due to the actions of local leaders, but due to demand on the international market and the power of multinational companies to manipulate prices, yet the view advocated by developing states, that political instability is caused by global inequality and balance of trade problems was given less attention in the Aga Khan report (see also Richards 1996, pp. 117–124). But it is, of course, impossible to disregard the impact of the global trade network that feeds the healthy 'Last Man' by sucking food and minerals out of the underdeveloped world while supplying it with the arms used to fight with increasing violence over the resources that remain. At the start of civil war in Chad, in 1966, 'there were almost no fighters, nothing to fight with, and no way to get to the fight' (Reyna 2003, p. 279). By Habré's rule in 1986–1987, 'there were perhaps 20,000 soldiers in different liberation armies armed with everything from tanks, to missiles, to phosphorous mortars. Habré may have had up to 25,000 people in his army' (Reyna 2003, pp. 276–7). In nineteenth-century Somalia, the most lethal weapon was the spear, but in 1992 'every man and youth I encountered was very visibly armed with a Kalashnikov, or American equivalent, and there appeared to be plenty of heavy weapons in the background' (Lewis 1997, p. 184). Keebet von Benda-Beckmann (2004), writing on recent violence on the Indonesian island of Ambon, states that imported guns and automatic weapons have increased the level of violence to a previously unknown level. The community to be defended has expanded from relatives and the village to the entire religious community. The elders no longer know whom to talk to, or how to re-create peace.

Bureaucratic governments are expensive to run. Given the low level of income created in their market economy and the state's limited ability to collect tax revenue, many African states cannot afford to sustain the bureaucratic government they inherited from the colonial era (compare Migdal 1988). In Kaplan's case, Hobbes is cited as an authority in order to distract attention away from Kaplan's failure to examine the international causes of the situation he portrays.

Pinker is also guilty of ignoring the impact of colonisation. Oblivious of the fact that the political chaos in central Africa is at least partly a legacy of the Belgian colonial quest for natural resources, he writes (2011, p. 307) that neither wealth nor peace come from having valuable things in the ground: 'Many poor and war-torn African countries are overflowing with gold, oil, diamonds, and strategic metals, while affluent and peaceful countries such as Belgium, Singapore and Hong Kong have no natural resources to speak of'. In support of his contention that deaths in war are declining, he quotes (2011, p. 51, citing Iraq Coalition Casualty Count, www.icasualities.org) the number of Americans killed in Iraq and Afghanistan in 2005 (that is, 945), but not the number of Iraqis killed by the USA. The heavy Iraqi death rate is only much later acknowledged (pp. 318–9). Pinker's source (Bohannon 2008) actually cites a higher estimate than Pinker's. The World Health Organisation, according to Bohannon, estimated 151,000 violent deaths in the 40 months following the allied invasion of Iraq, a rate of 45,300 per 12 months.

8.5.2 Pinker

In his earlier account (2002), Pinker misunderstands the Prisoner's Dilemma. He does not make it clear that a zero-sum game can be transformed into a non-zero-sum game within the 'rules of the game', building mutual trust without an umpire. His 2002 account of the Prisoner's Dilemma only tells the first part of the story, where the prisoners lack the opportunity to build trust: 'the optimal strategy for each prisoner is to defect' (2002, p. 334)—the Hobbesian condition. He wrongly claims 'The only way to win the Prisoner's Dilemma is to change the rules or find a way out of the game' (p. 335). Ross (2012, accessed 27/01/2012) interprets Hobbes's argument as an early example of game theory. 'The structure of his argument is that the logic of strategic interaction leaves only two general political outcomes possible: tyranny and anarchy'—the outcome of Prisoner's Dilemma in situations where no trust can develop. This makes Hobbes an appropriate authority for Pinker.

Pinker's conclusion in 2002 is particularly puzzling because before reaching it he cites one of the most remarkable cases of mutual trust built without the intervention of a sovereign, the emergence of the precisely timed artillery barrages during World War I that allowed both British and German troops to predict when it was safe to move. Officers exercised autocratic authority and yet had considerable trouble bringing the practice to an end and destroying mutual trust (see Trivers 1985, pp. 362–3).

The most significant change in Pinker's position in his 2011 book, is that he now understands the importance of the iterated Prisoner's Dilemma which, he notes (2011, p. 533), 'can even be a good model for the evolution of co-operation'. Pinker does not, however, recognise that hunter-gatherers are acting out the iterated Prisoner's Dilemma in their strategies for sustaining inter-band relationships. Rather, he finds the origin of such strategies in the transparency and intelligibility of a free market economy, or 'gentle commerce' (2011, p. 287). This advance in Pinker's analysis enables him to recognise the value of democratic leviathans. To take advantage of the opportunities of trade, people had to plan for the future, control their violent impulses, take other peoples' perspectives into account and exercise the cognitive skills needed to prosper in social networks. The Better Angels of empathy, self-control, morality and reason render autocratic leviathans less necessary, and the state's role need only be to punish aggressors, to cancel out their gains (p. 680). With a characteristically rhetorical turn of phrase, he notes:

> Libertarians, anarchists, and other sceptics of the Leviathan point out that when communities are left to their own devices, they often develop norms of cooperation that allow them to settle their disputes non-violently, without laws…or the other trappings of government. (2011, p. 79)

But, he counters, these cases do not obviate the need for government.

Pinker remains guilty of a larger misunderstanding of social anthropology. It is important to be clear that, contrary to Pinker's claim concerning 'the blank slate' (2002, pp. 23–4), Durkheim did not deny the existence of psychological phenomena. His argument was that their study fell outside the realm of the social sciences. French language, currency and laws '…should not be confused with biological phenomena, since they consist of representations and of actions; *nor with psychological phenomena, which exist only in the individual consciousness*' (1938, p. 3, my emphasis).

Durkheim's juxtaposition of psychology and sociology is exemplified by his ([1952/1897]) theory of suicide. Suicide, he argued, is not precipitated simply by one individual copying other individuals who have already killed themselves, as his rival Tarde might have claimed. Some people are weakly integrated into society, others are highly patriotic. Durkheim postulated that when social relations are eroded, the former are more likely to commit suicide, through a sense of isolation. When social relations are particularly close-knit, as during war, the latter are more likely to commit suicide, giving their lives to save others. The sociological phenomenon was the correlation between suicide rates and the relative coherence of society. A similar argument can be advanced with regard to human violence; the level of violence depends on the character of the social environment. Pinker does not consider that in a highly social species such as ours, where we depend entirely on relationships with other people, the urge to make peace may be as strong, and as deeply rooted in psychology, as the urge to violence. It is the shape of the social 'fitness landscape' that determines the success or failure of such competing strategies.

8.6 Practical Implications

Policy and practice for the resolution of conflict have a vital impact on human wellbeing. Policies derived from Hobbes are based on the assumption that men are incapable of peaceful co-operation without the oversight of an autocratic government. But what kind of an authority does Hobbes provide? To show his relevance, one must demonstrate that the particular conditions he specified are universally true. To admit the possibility of other scenarios would undermine Pinker and Kaplan's arguments for inevitability and/or genetic determinism. Instead, these authors assert the truth of Hobbes's axiom in order to bypass contrary evidence and conclude that autocratic government is the only guarantor of peace.

Yet, empirical research demonstrates that people are not by nature either peaceful or warlike; some conditions lead to war, others do not (McGuire 2002, p. 141). A stable nation state can greatly reduce the level of violence. In the French village of 'Pellaport' that I studied between 1969 and 1995 (Layton 2000), two suicides occurred but no murders were committed over that quarter century, in a population that fluctuated between 250 and 300. Yet a bureaucratic state of the form defined by Weber (1947) is costly. Many states in the global South cannot afford such organisation. A peasant economy generates little cash surplus, tax revenues are extracted by local leaders, multinationals avoid paying tax and little income may pass up to the centre. The quasi-feudal form of state that emerges is a cheaper but less stable alternative to Weberian bureaucracy. While Weber, following Hobbes, advocated that the state should hold a monopoly on violence, armaments supplied by foreign powers to weak African and Asian states may increase the level of violence, as the cases of Chad, Somalia and Indonesia demonstrate. The nation state can be a mixed blessing. Hobbes' a priori reasoning and Kaplan's Orientalism must be replaced by a consideration of the rationality of different social adaptations in different ecological and social contexts.

The theory of games provides a more nuanced approach to the specific conditions that are likely to engender conflict and how trust might be restored (for case studies, see Leutloff-Grandits 2003; Barakat et al. 2001). Where the state fails to provide adequate protection, people will turn to more localised and trustworthy support networks, among which the idiom of kinship is frequently prominent (e.g. Al-Mohammad 2010; McGovern 2012). Ethnic or religious leaders seeking a greater share of resources for their group will assert that they are confronted with a zero-sum game (see, for example, Denich 1994; Rao and Reddy 2001); peacekeepers should seek to demonstrate that there is, on the contrary, a non-zero-sum game to be played. Providing reliable and trustworthy sources of information about the intentions of other players in the wider society within which small communities are embedded may be crucial.

If a Western state were planning to send its army into a country such as Iraq, Afghanistan or Syria today, to create peace, it would be imperative to examine the shape of the social fitness landscape within which local people are choosing, or are likely to choose, particular strategies of conflict or co-operation:

- What is the network of social relationships on which local people depend for their livelihood, and what relationships would they be likely to repudiate?
- What resources are valuable and accessible enough for local people to consider them worth fighting for?
- What level of taxation can be raised from legitimate local economic transactions?
- Where do taxes currently go, and how can they be transferred to the state?
- What level of public services can be delivered through reasonable salaries to state personnel, given the available tax income?

If aid fails to bring about peace or prosperity, it is more likely that it facilitated or entrenched social division, rather than that it was intrinsically unproductive

(Pottier 1996; Wedel 1998). The UK government has, since 2004, been developing a 'Stabilisation Unit' within the Department for International Development. This unit maintains a website http://www.stabilisationunit.gov.uk/stabilisation-and-conflict-resources.html (accessed 26/11/2012) that contains a valuable collection of up-to-date studies offering lessons learned from recent exercises in peacekeeping and conflict prevention. While the relationship of these reports to UK government policy should be kept in mind, this source is highly recommended.

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Chapter 9
Understanding and Addressing Cultural Variation in Costly Antisocial Punishment

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Abstract Altruistic punishment (AP)—punishment of those contributing little to the public good—has been proposed as an explanation for the extraordinary extent of human culture relative to other species. AP is seen as supporting the high levels of altruism necessary for the cooperation underlying this culture, including information exchange. However, humans will also sometimes punish those who contribute greatly to the public good, even when those contributions directly benefit the punisher. This behaviour—antisocial punishment (ASP)—is negatively correlated with gross domestic product, and may be a hindrance to overall wellbeing. In this chapter, we pursue a better understanding of ASP in particular and costly punishment in general. We explore existing data showing cultural variation in the propensity to punish, and ask how such sanctioning, whether of those who give much or little, affects the individuals who conduct it. We hypothesise that costly punishment is a mechanism for regulating investment between different levels of society, for example, whether an individual's current focus should be on their nation, village, family or self. We suggest that people are less likely to antisocially punish those they consider to be 'ingroup' and that the propensity to apply this identity to strangers may vary with socio-economic–political context and resulting individual experience. In particular, an increased propensity to express ASP should correlate with a lower probability of benefiting from public goods, as may be the case where there is a low rule of law. We show analysis of both behavioural economics experiments and evolutionary social simulations to support our hypotheses and suggest implications for policymakers and other organisations that may wish to intervene to improve general economic wellbeing.

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9.1 Introduction

> That friendship lasts longest—if there is a chance of its being a success—in which friends both give and receive gifts.—*The Hávamál*[1]

The variety of human cultures is one of the joys of contemporary human life. However, a respect and appreciation for diversity cannot be allowed to mask the observation that cultural variation can include measurable differences in metrics that have nearly universal cross-cultural appeal, for example, reducing infant mortality or increasing literacy. For the past several years, we have been striving to understand cultural variation in one such trait: the propensity of individuals to optimise economic collaboration when thrown into a group together. In this chapter, we review our progress to date. We also examine the policy implications of our findings on cooperation and punishment, particularly for organisations wishing to aid development or rebuild communities in areas experiencing conflict.

The behaviour we are studying is called *antisocial punishment* (ASP). Technically, ASP occurs when an individual is willing to pay a penalty to punish a member of their own group, where the victim of the punishment has been generous, providing *more or equal* contributions to their mutual group than the punisher. The term *punishment* here is being used to describe a punisher deliberately paying a cost to have money taken away from the victim of their punishment. For the data analysed here, this is all done anonymously in an experimental context, with the experimenter acting as the go-between, executing the instructions of the participants. In ordinary experience, we believe this behaviour to map to the situation where generosity or philanthropy is rejected, resented or punished. In sociology, this relates to the theory of the gift, where healthy equal exchange increases bonds, but gifts that cannot or will not be reciprocated are seen as a power move, an extreme version of which is potlatch (Mauss 1967).

Systematic cultural variation in ASP behaviour was first documented in the economics literature by Herrmann et al. (2008a), and Benedikt Herrmann has been one of our collaborators throughout this project. Although the data Herrmann et al. provided are based on formal laboratory experiments where participants play a 'game' for money, the results correlate highly with national gross domestic product (GDP), suggesting the possibility that the behaviour measured in the laboratory may have fundamental impact on the economic wellbeing of a nation, though of course the reverse could also be true. Further, the variation between cultures is not arbitrary, but rather appears clustered by global region. Thus Boston, several cities in Northern Europe, the Far East and Melbourne show high levels of profitable economic collaboration, while Athens, Istanbul, regions of the Middle East and of the former Soviet Union show relatively low ability to collaborate for profit, and higher levels of ASP.

If we can find an explanation for such variation, we might not only be rewarded with a better understanding of culture and society more generally. We might also be in a better situation to administer economic aid, or to otherwise shape intervention

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[1] Translated by Martin Clarke (1923), also quoted by Mauss (1967).

policies. If generosity is perceived as a power move to be resented and, if possible, rejected, then clearly it is less likely to be effective. How can we cause interventions to be perceived as a collaborative effort to mutually improve economies and/or security? In the present chapter, our focus is at the level of the city and state, but this work is also relevant to managing interpersonal relationships and individual socialisation and wellbeing.

This chapter begins with a review of the scientific context of our research. We then review our findings, some of which have been published previously, others of which are presented here for the first time. Overall, we have failed to find any evolutionary context in which ASP can evolve unless we assume that it carries some extra benefit beyond its economic costs. We hypothesise that this benefit is social status awarded to those who punish. In the results given here, we model the simplest case, which is awarding status regardless of whether the punishment is altruistic (punishing those donating less than the punisher to the group) or antisocial.[2] If we include this assumption, then we *are* able to account for variation in ASP. We suggest that regional variation in ASP reflects the extent to which in various societies one's wellbeing depends on one's relative status within one's own group rather than the group's status in relation to other groups. After reviewing these findings, we discuss policy implications for our work. We make a number of suggestions and then close with our conclusions.

9.2 Scientific Background: Costly Punishment

Herrmann et al. (2008a) show that in some human subject pools (e.g. university undergraduates in Boston, Melbourne, Chengdu and Zurich) group members tend to quickly exploit an experimental context in which mutual investment leads to mutual benefits. However, in other societies (e.g. university undergraduates in Muscat, Istanbul, Minsk and Athens) substantial proportions of participants will pay a fee in order to penalize group members more generous to the group's public good than themselves. This is despite the fact that this generosity is benefiting all group members *other than* the benefactor, including the punisher. Such punishment of cooperation is called ASP.

Herrmann et al. sought correlates for the prevalence of ASP in a culture, finding several. ASP inversely correlates with both gross domestic product (GDP) and the rule of law (Kaufmann et al. 2004). They suggest that 'weak norms of civic cooperation and the weakness of the rule of law in a country are significant predictors of antisocial punishment. Our results show that […] punishment opportunities are socially beneficial only if complemented by strong social norms of cooperation.' But correlation does not demonstrate causation. Can we be sure that the propensity for ASP does not itself lead to a weak rule of law? Or that both could be caused by some other factor? In the next section, we describe the data in greater detail and try to answer these questions.

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[2] Of course, reality could be more subtle (Barclay 2006; Sylwester et al. 2013).

9.2.1 The Data: How Cooperation and Punishment are Measured

All human subject data for this research were collected using a paradigm from a relatively new branch of economics called either *experimental economics* or *behavioural economics*. Behavioural economics is similar to experimental psychology, except that economists mandate certain conditions, for example, all individuals must receive sufficient financial reward to be considered motivated. Significantly, subjects can in no way be deceived and must in fact demonstrate understanding of the complete consequences of their own and the other team members' possible actions by passing a test before participating in the games. Similarly, in cross-cultural experimental economics research, the players play for tokens to keep reasoning about proportions equally easy for subjects regardless of local currency denominations (Herrmann et al. 2008b).

The standard behavioural economics experiment for assessing costly punishment is called the public goods game (PGG; Ledyard 1995). In the basic form of this game, there is no punishment. In the standard form, a group is determined by an experimenter, but members are not identified to each other and only interact by computer screens.[3] This anonymity simplifies theoretical analysis by ensuring that group members do not act out of fear or expectation of retribution or reward after the game. In a single round of PGG, each member is given 20 tokens by the experimenter. Subjects are then allowed to contribute any portion they choose of their allocation to the public pool. Allocations to the public pool are multiplied by the experimenter and then divided equally between all group members. The multiplication factor is always greater than one but smaller than the number of group members. As a result, the optimal outcome for the group as a whole is for all to contribute everything, but *individual* investments are never fully returned. For example, if the multiplier is 3 and the number of individuals is 4, then for every token an individual donates, they (and every other member of the group) receive 3/4 of a token back. Thus, individuals who do not contribute anything or contribute less than others gain a financial advantage relative to those others, at least for that round. A PGG therefore represents a social dilemma because an individual's interests are in conflict with their group's. In the experiments described below, PGGs are played repeatedly for ten consecutive rounds with the same groups.

In the form of the game allowing punishment, after a round of PGG individuals can anonymously punish others. The target to be punished can be identified only by their previous round's contribution to the public pool. Importantly, subjects never learn any information about who punishes them. Punishment is costly; in the studies described here, for every token a punisher pays, the punishee loses three tokens.[4] When an individual punishes someone who has contributed less than they have, this

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[3] In rural conditions, the computers may be replaced with pen and paper for recording decisions, and then the results are communicated to group members by the experimenter.

[4] Many other cost/effect ratios have been tried by other experimenters; these result in quantitative but not qualitative shifts in behaviour. See Sylwester et al. (2013) for a more complete review.

punishment is termed *altruistic punishment* (AP) because the punisher pays a cost, yet the whole group benefits if (as seems often to be the case) this action leads to higher contributions. On the other hand, if punishers punish those who contribute more or equally to themselves, the punishment is called *antisocial*. Herrmann et al. (2008a) were the first to document societies with large amounts of ASP, and showed that this could in some cases completely counter the expected benefits of allowing punishment, in fact reducing overall cooperation and payoffs to the subjects compared to non-punishment conditions. In the Swiss contexts where these experiments were first run, the opportunity to punish reliably resulted in a better economic outcome for subjects playing the PGG. However, this was not true in some societies with high levels of ASP. In most of the data reported here (all of which are due to Herrmann et al.), subjects played two sets of ten PGG, one with punishment and one without. For most subject pools, the order of the sets of games (punishment or not) was randomised.

9.2.2 Previous Interpretations of Punishment Results

To fully understand the literature and history of work in costly punishment, we must recognise that one goal of anthropology is explaining human uniqueness. Why are humans the only species with advanced technology? Why are we dominating the biomass of the planet with our ever-expanding population? The explanation is not simple biology—it is not just our intelligence or our capacity for tool use. The vast majority of population growth and technological complexity is of very recent origin. Very human-like species existed and used primitive tools for millions of years (Walker and Stringer 2010). Urbanisation, agriculture, writing and doctrinal religions (those that share their practices outside of small close-knit tribal structures) all seem to date to no more than 8,000–12,000 years ago, well after the first appearance of *Homo sapiens*.

Numerous empirical and theoretical studies have suggested or proposed an extraordinary human propensity for cooperation as an explanation for the extent of human culture (e.g. Gintis et al. 2003; Henrich et al. 2001). However, the reasoning could just as easily be applied in reverse; it could be that an extraordinary human propensity for accumulating culture accounts for the extent of human cooperation (Bryson 2009). Thus, the extent of human cooperation is not yet considered fully accounted for. After the early PGG punishment results (e.g. Fehr and Gächter 2000; Fehr and Gächter 2002), AP was regarded as a possible explanation for large-scale cooperation. Here too though the reasoning seems cyclic, as punishment can be a form of cooperation itself, and, contrary to its reputation, altruistic behaviour is neither difficult to evolve nor uniquely human (Čače and Bryson 2007; West et al. 2007; MacLean et al. 2010). Swinging to the other extreme, the phenomenon of ASP has more recently led some scientists to emphasise the ‘dark side’ of human behaviour, including a tendency for spite and hyper-competitiveness (Abbink and Sadrieh 2009; Jensen 2010; Sylwester et al. 2013). Extremes of moral assessment and defensiveness need to be guarded against if we are to understand what underlies these phenomena. We believe the Herrmann et al. (2008a) results indicate that punishment is part of a much more complex system of social regulation, not a simple explanation for human cooperation and therefore culture. Here, we attempt to approach the explanation of costly punishment objectively, by viewing both cooperation and punishment as biological phenomena and looking for ultimate causes that might make such behaviour adaptive. In the next section, we briefly review the sorts of explanations natural selection can provide for behaviour.

9.2.3 Proximate and Ultimate Explanations

Fields like evolutionary anthropology and behavioural ecology work from the assumption that behaviour is inseparable from the rest of the organism, including in terms of its causal explanation. From the perspective of evolution, there are at least two types of causes for any trait (Mayr 1961). Ultimate causes concern why the behaviour is present in a population as whole—what role does it serve in the evolutionary struggle? Contemporary evolutionary theory does not expect all observed traits to be adaptations—some are incidental side effects of historical associations, since the selection process takes time and can only operate on the material at hand. Nevertheless, it is at least a common first guess in evolutionary approaches that an observed trait exists because it has historically provided more advantage than disadvantage to those who hold it relative to those who do not. Proximate causes in contrast describe mechanism—what triggers and/or enables a particular organism to perform the behaviour in question. For example, running may be ultimately a good way to escape and proximately a response to a loud noise. Note that for some species, flying or swimming is a better mode of escape than running. Identifying the ultimate cause of a behaviour does not mean that behaviour is necessarily the optimal mechanism for meeting that need. Which behaviour will be expressed also depends on evolutionary (phylogenetic) history.

A useful proximate mechanism may itself become an ultimate explanation for some other trait. For example, hearing the sound of a predator may be the proximate cause of fleeing, *and* the ultimate cause for large ears. This sort of complexity has led some to suggest that the distinction between these causes is not real and creates an impediment to understanding (e.g. Thierry 2005; Laland et al. 2011). However, the distinction was developed to address a still-common error—thinking that a simple proximate explanation for a behaviour can displace a complex ultimate one. While science generally favours simpler explanations, because proximate and ultimate explanations address different questions, one cannot substitute for the other.

9.3 Building an Understanding of Antisocial Investment

In this section, we introduce our findings concerning an explanation for the behaviour termed *ASP*. We begin by explaining our current hypothesis and then review the evidence we have discovered leading us to this hypothesis.

9.3.1 Hypothesis: Punishment as Regulation

Our current hypothesis is that all punishment is an aggressive act, which some proportion of any population is motivated to perform. A proximate reward for aggression is increased social status, not only relative to the target of the aggressive act but also relative to bystanders who witness the aggression. When an individual becomes known to be aggressive, confronting that individual becomes associated with an increased cost, thus making avoiding confrontation via submissive gestures a more attractive strategy (Preuschoft and van Schaik 2000). We also hypothesise, however, that in contexts where cooperation is more likely to produce stable public goods, members of the population are also more likely to inhibit any tendency they might feel to be aggressive towards cooperators. We hypothesise that for at least some proportion of the population, whether cooperative gestures are accepted as useful or seen as another form of dominance/aggression depends on whether the generous individual is seen as a member of a trusted 'ingroup' or is seen as 'outgroup'—a potential invader. Thus, the proximate explanation for a population with relatively high ASP is a larger number of individuals assessing anonymous strangers playing a PGG as outgroup, and the ultimate explanation is a dependency on the expected utility of public goods in that population's socio-political-economic context. This expected utility is estimated by the individuals composing the population based on data from the experience of their lives up until the experiment, as interpreted through prior expectations communicated to those individuals by their culture, which reflects the experience of many more individuals.

Our hypothesised ultimate benefit derives from the observation that an investment in a global public good comes at a cost of reduced investment not only directly to the individual but also to other more-local goods such as the individual's family. The ultimate need to support many levels of investment may explain the otherwise odd tendency of nearly all subjects to split their investment strategy, keeping some proportion of the resources originally allocated to them by the experimenter and investing the rest. When Northern Europeans (including Boston in the Herrmann et al. data) read the instructions concerning the punishment condition of the PGG, their expected utility allocated to the public good immediately increases. Interestingly, in the three cities tested in Australia and Asia, the initial expectation seems to be the same in both conditions, but that expectation rises over the course of the multi-round game in response to increased revenue as rounds are played. Whereas for Athens, Istanbul, the Middle East and the former Soviet Union, neither expectations nor rewards increase, and public goods investment stays approximately constant at a relatively low level throughout.

Thus at an ultimate level, we hypothesise that variation in punishment strategies may be an evolved mechanism for regulating global public goods investment (versus more-local or individual investment) to a level appropriate to that population's economic context. What is appropriate is estimated in a distributed fashion by the population's individual experiences and aggregated into a set of collective norms and expectations that influence proximate responses to social dilemmas.

In the remainder of this section, we review our evidence for this hypothesis. Where we describe human data results, these are derived from further analysis of the original Herrmann et al. (2008a) data. The additional analysis was performed mostly by Sylwester and Mitchell. However, we first turn to theoretical results derived from simulation. Simulation is a process of analysing the full consequences of a theory by describing it so thoroughly that it can be executed on a computer. All systems of modelling theory are analytic processes performed because, as Kokko (2007) phrases it, 'our brains aren't big enough' to see all of our theories' consequences. Thus, for example, different researchers might dispute whether a minimalist theory is really sufficient to explain the complex behaviour observed in the real world. Formal modelling can demonstrate with certainty whether the results of a hypothesised system are as predicted, though it *cannot* determine with certainty whether this reflects what happens in the real world. Models are ultimately only theories, and their validity is assessed by standard scientific processes of assessing fit to data and evaluating unexpected predictions (see further in Bryson et al. 2012; Whitehouse et al. 2012). Computer modelling (simulations) also allows us to check for internal coherence of our theories, since inconsistent theories are impossible to build and run as programs.

Most of the modelling performed here is a form of simulation known as agent-based modelling (ABM). That is, abstracted versions of both the individual actors (agents) and the environment in which they act are programmed into computers. The abstractions include the hypothesised minimal set of actions the agents are capable of, knowledge the agents must retain to inform this action, elements of the environment (including other agents) the agents may act on, and the results of these actions. A computer then executes the operation of the agents over time and reports the consequences. Where these are not completely deterministic, many experimental runs may be performed to discover the probable distribution of results. Where characteristic of the agents or environment are not known or believed to vary, again many runs can be performed with different values of these, to measure the consequences. Here, most of the described modelling has been performed by Powers and Taylor.

9.3.2 Ultimately, ASP is not Viable Unless it Correlates with Some Other Benefit

We begin our presentation of evidence for our hypotheses by examining the basic question of the circumstances in which punishment could have evolved as a strategy. The results presented here are based on multilevel evolutionary ABM. A multilevel model allows us to manipulate the relative costs and benefits of within-group and between-group competition. This is one way to think about local versus global (in the biological sense of 'global' as 'less-local') investment and competition. Local competition occurs *within* the ingroup—for example, who in my family gets the biggest piece of pie? In contrast, global competition occurs between groups—for example, which family gets the most pies? Note that there can be many levels of competition and therefore selection. Families can join together to compete as one village against another; villages may join to compete as one state against another.

The multilevel ABM here extends from Powers et al. (2011). Within-group competition is increased by *increasing* the group size, since this increases the variance in social behaviour *within* groups, and so increases the strength of within-group selection. Between-group competition is likewise increased by *decreasing* group size, since this increases the variance in social behaviour *between* groups, and so increases the strength of between-group selection. The importance of between-group competition is also increased by *decreasing* the probability that individual agents find themselves in new groups, that is, by reducing the frequency with which groups are reformed. This may be thought of as modelling a decreased amount of communication and interdependency between groups in the real world, e.g. little intermarriage. Note that both mechanisms serve as abstractions and may represent more complex real-world variations in rewards at the different levels. For example, climate change could increase population pressure by reducing the amount of habitable territory. This could result in increased migration between groups, changing the scale of competition from more local to more global.

Here, we examine the viability of ASP in particular as a strategy, and also how its availability as a strategy affects the utility of costly punishment as a strategy overall (Powers et al. 2012). A linear PGG with punishment is played within groups once per generation. The payoffs from this game determine the fitness of individuals, such that individuals with a high absolute payoff produce more offspring. Groups remain together for a particular number of generations. Then all individuals are considered a part of one global migrant pool from which the next generation of groups is formed. This so-called *dispersal stage* creates between-group competition, since groups containing a larger number of individuals at the time of dispersal produce a larger fraction of the migrant pool, and hence have more impact in the next generation of groups. The size of a group at the time of dispersal is in turn affected by the mean payoff that its members receive from the PGG.

In a thorough examination, Powers et al. could find no evolutionary context in which ASP was adaptive against other social strategies, unless we assume that punishment actually has a *negative* cost. That is, punishment must generate some benefit to the punisher in order for ASP to ever be adaptive. However, as explained earlier, punishment is by definition costly and also, relative to other group members, altruistic, since any economic benefit accrued to the punisher due to, e.g. an increase in PG investment is shared by the others even though they do not pay the cost of punishment. One example of how punishment might benefit the punisher despite costing risk of injury, effort and time is if punishment takes the form of taking resources away from the target. If the punisher keeps these for himself rather than sharing with the rest of the group, this would compensate immediately for the risk of aggression (Taylor & Bryson, unpublished). However, even where the proximate outcome of punishment is fully public, there may be other longer-term benefits to the punisher, such as increased social status and its associated benefits (Preuschoft and van Schaik 2000). We know that AP in ingroup contexts does lead to increased status (Barclay 2006; Sylwester and Roberts 2010).

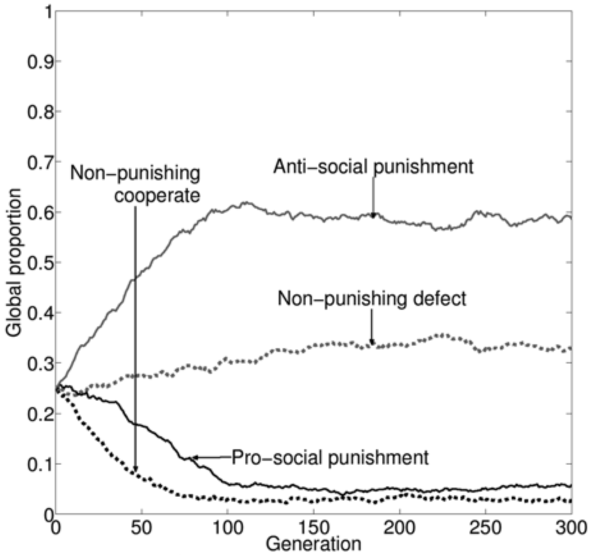
Our current guess is this latter option—that punishment is used to signal or even generate dominance within a group. The benefits of social dominance over the lifetime of the punisher may more than compensate for the immediate cost of the punishment act (West et al. 2011). Indeed, dominance is often seen as a form of long-term conflict resolution, because it reifies a particular set of expectations of conflict outcome, thus reducing the amount of actual physical conflict required (Preuschoft and van Schaik 2000; Bryson et al. 2012). Thus, both AP and ASP may maintain or increase an individual's rank in a dominance hierarchy, which may in turn increase long-term benefit and thus fitness relative to those who do not (Clutton-Brock and Parker 1995; Boehm 1999; Rohwer 2007). But this guess has yet to be turned into a formal hypothesis, let alone tested. What we know from our simulations is only that *some* additional factor must account for the existence of ASP.

Even in the case where punishment *does* result in intrinsic benefit, then there is still an impact of local versus global competition. Where groups compete with each other—in the present ABM, where they persist long enough to receive fitness payoff for their public goods —prosocial (altruistic) punishment is still selected for over ASP (Fig. 9.1a). Only when within-group competition is the stronger selective force can even individually advantageous ASP outcompete the other form of punishment (Fig. 9.1b).

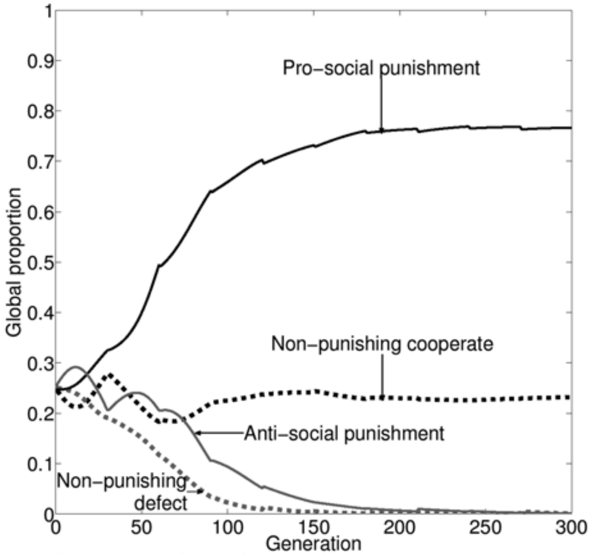
9.3.3 Punishment Alone Cannot Account for Human Sociality

As described in Sect. 9.2.2, the finding by Herrmann et al. (2008a), that populations exist in which the introduction of punishment reduces performance in PGG, was disruptive to those who believed that punishment explained exceptional levels of cooperation in humans. This result is sufficiently disruptive that it has been attacked on methodological grounds, either against behavioural economics in general or as practiced in the specific cases. However, modelling results show that even in pure theory, once ASP is taken into account, punishment cannot be considered solely a mechanism for increasing cooperation (Rand et al. 2010; Rand and Nowak 2011; Powers et al. 2012).

As Fig. 9.2a demonstrates, even where punishment is exclusively altruistic, cooperation will not necessarily be selected for. Only where group size is relatively small and relatively stable (there are many generations between dispersal stages) do cooperative strategies reliably evolve. This is because such conditions increase the variance in social behaviour between groups (see Powers et al. 2012), and so create conditions for effective group selection. As a result, cooperation (including AP) is more likely to be a beneficial strategy and increase in prevalence. Conversely, a large founding group size and/or frequent group mixing increases within-group variation in social behaviour, and hence makes within-group competition a larger driver of the evolutionary dynamics. In such cases, defection and ASP are favoured. Figure 9.2b shows us that introducing ASP reduces the evolutionary contexts where cooperation is favoured even further.

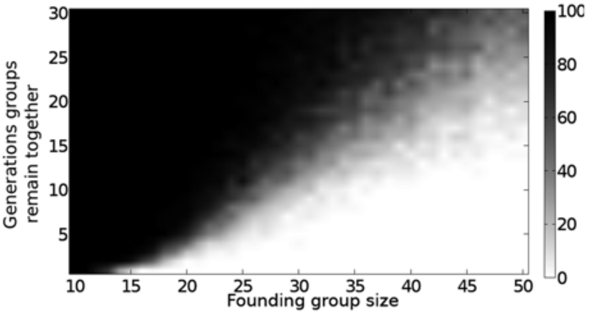


(a) Groups reform every generation.

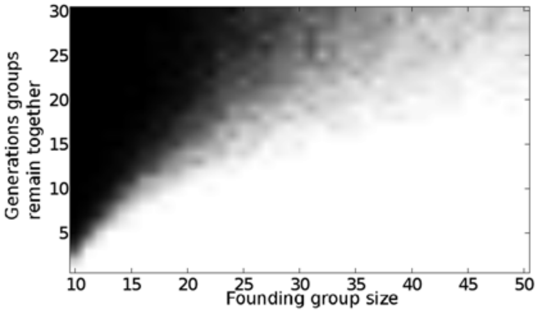


(b) Groups reform after 30 generations.

Fig. 9.1 Evolution of strategy frequencies given that punishment provides direct benefit. ***a*** When groups reform frequently, within-group competition is the main driver of the evolutionary dynamics. Parameters: founding group size $=15$, benefit from cooperation $=0.9$, cost to cooperating $=0.1$, cost of being punished $=0.3$, cost of punishing $=-0.1$, groups randomly reformed every generation. **b** When groups stay together for multiple generations, between-group competition supports cooperative strategies. Parameters: As for **a**, but with groups reforming every 30 generations.



(a) Only altruistic punishment possible.



(b) Both altruistic and antisocial punishment possible.

Fig. 9.2 Percentage of Monte Carlo simulation runs in which individuals exploiting prosocial punishment and cooperation together constituted more than 90% of the global population at equilibrium: **a** without the presence of antisocial punishment; **b** with antisocial punishment included. Note here (unlike Fig. 9.1) punishment is assumed to be costly; thus, ASP never dominates as a strategy, yet its impact is still significant. A small founding group size and/or infrequent group mixing increases the variance in social behaviour between groups, and thus makes between-group competition a major driver of the evolutionary dynamics. (After Fig. 3 of Powers et al. 2012)

Punishment is by no means required for cooperation. That cooperation is adaptive in a wide range of circumstances has been long understood. In fact, cooperation between replicators is necessary for the existence of any organism with more than one gene—that is, for all life (Dawkins 1982). It is even easier to explain in multigene organisms (Hamilton 1964). In our opinion, the most interesting implication of our simulations is that at an ultimate level, punishment can be used to *either* increase or decrease cooperative investment in public goods. In contexts where investment at the group level is unlikely to be beneficial (e.g. where public goods are likely to be confiscated by other groups before they are exploited), members of the group may receive better inclusive fitness benefits from more direct investment, e.g. in offspring. This opens the door to the possibility that the proximate mechanisms that lead to punishment serve ultimately as a distributed mechanism for regulating the level of investment populations make to that most appropriate for the individual's socio-economic context.

9.3.4 Proximate Causes and Consequences of ASP

We now move from ultimate causes and simulations to proximate mechanisms and explorations of real human data. The first thing worth noting is that the terminology behind ASP and AP can be quite misleading (Sylwester et al. 2013, unpublished). Firstly, 'AP' is not generally altruistic in intention. Proximately, costly punishment is frequently motivated by aggressive tendencies. Secondly, ASP is not always aimed at the top contributors and cannot be ascribed entirely to revenge. ASP occurs even in the first round, before anyone has been punished. Sometimes ASP is aimed from the lowest contributor to the second-lowest contributor, in an apparent effort to make them produce more public goods while allowing the punisher to continue to freeride. When this occurs, ASP can actually be seen as an altruistic act, because the punisher pays a penalty, and the other members of the group (those who are not the punishee) benefit just as much as the punisher if the punishee increases their contribution. In fact, those who never punish (a sizeable minority) could also be seen as freeriders in cultures where punishment leads to an increase in the public good.

The fact that this terminology is misleading does not mean it should be abandoned. ASP and AP both have clear definitions (as given in our Introduction, Sect. 9.1) and clearly correlates with important measures of economic wellbeing (as demonstrated by Herrmann et al. 2008a). But we need to remember not to associate the obvious moralistic assessments with these terms, and more generally that socio-economic behaviour, dependencies and outcomes are highly complex. Further, as has often been noted, most contemporary human experimental subjects are university undergraduates, and universities have historically been most prominent in countries that are high in indices such a wealth, democracy and rule of law (Henrich et al. 2010). As Herrmann et al. (2008a) have shown, these societies express relatively little ASP, and as a consequence ASP has been regarded as a marginal phenomenon, perhaps explicable simply as revenge taken by those punished altruistically (Fehr and Gächter 2002).

One might expect that ASP would lead directly to reduced contributions just as AP leads to increases, but in fact victims' responses to ASP are much less directed than victims' responses to AP (Sylwester et al. unpublished). This indicates that the evolutionary 'strategy' associated with punishment expression may well include the punishment response. Without punishment, nearly 80 % of individuals maintain from one round to the next their previous level of investment in the public good. However, among victims of ASP, the number maintaining their previous round's strategy falls to nearly 40 %, though the direction of change shows no clear pattern. In contrast, victims of AP reduce their probability of repeating their investment level to only 20 % and are much more likely to increase investment than to decrease it. These results are despite the fact that the individuals in these experiments do not know who punished them, and therefore often cannot determine certainly whether their punishment was altruistic or antisocial.[5] However, note that subjects with very low or very high prior levels of investment have only one direction to change in.

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[5] Of course, one in four individuals give the least in their group, so know any punishment is altruistic, and the same number contribute the most and know theirs is antisocial.

Given our hypothesis that punishment's expression may be determined by ingroup/outgroup assessment, we can mine a great deal of psychological literature for candidate proximate causes in the form of cues that trigger shifts in these assessments. Sylwester et al. (2013) explain that we would expect AP to be less useful when applied to members of outgroups, since it might prompt members of other groups to behave more cooperatively, thus decreasing the punisher's own group's relative ranking and therefore (presumably, if there is group-level competition) resources. Conversely, we would expect ASP to be practiced less in contexts where the other group members are assessed as 'ingroup'. Lamba and Mace (2012) show empirical evidence supporting this idea. In extremely similar but discrete populations of a very small-scale minority culture in India (the Pahari Korwa), Lamba and Mace demonstrate lower levels of ASP in villages that contain a higher proportion of other cultures as well, compared to villages exclusively composed of Pahari Korwa. This may indicate that the presence in a village of a potential outgroup leads subjects of a game played between members of a single culture to treat each other as ingroup. But where the criteria for selection of experiment participation was not so clearly ethnic (due to only one ethnicity being present in the village), subjects were more likely to view each other more as potential competitors.

9.3.5 Individual Strategies: Variation in ASP is Best Predicted by Proportions of Highly Cooperative Actors

Not every individual in a population will necessarily express the same behavioural strategy in the same immediate context. As explained earlier, we hypothesise that at a population level, the ultimate explanation of variation in punishment strategies and their associated economic productivity is an optimising response to local political and economic conditions which can determine the expected outcome of a public good investment. Therefore, we should expect that whatever the proximate mechanism for selecting an investment (including punishment) strategy is, it should respond to evidence or experience indicating changes in this underlying context. Presumably, each individual responds to their own individual experience, though this may include the stories they hear from others and their upbringing. Their exact response may also be determined by other predispositions such as personality or self-assessed social ranking.

Note therefore that we do not need to expect everyone in a population to express the same strategy at the same time. We only expect that first, the net result of combining these strategies in the proportions found in a population tracks the underlying context, and that second, each of the strategies should be self-sustaining to the extent they are expressed within that context. MacLean et al. (2010) document how for even very simple organisms in a simple environment, it may be easiest to optimise exploitation of that environment by altering the number of individuals expressing prosocial or antisocial behaviour, in the form of investing in or freeriding on public goods.

If AP really did account for cooperative behaviour, we might expect its prevalence to correlate with economic performance and that of freeriding to be anticorrelated. In fact, we find no such thing. In examining the data set due to Herrmann et al. (2008a), we found both freeriding and AP to be fairly consistent across populations. What varies with regional economic performance as measured by GDP is the proportion of strong cooperators in a society (defined below) and the propensity to antisocially punish cooperators.

To better understand correlates of decreased public investment, we explored the hypothesis that subject pools might differ in the composition of cooperative types. For clarity (and after some experimentation), we focussed on distinguishing just two classes of extreme behavioural types from among the participants. Our classification was based on participants' behaviour in the very first round of the first PGG they played, including cases where no punishment was allowed. All behavioural economics subjects must demonstrate full comprehension of a task in a test before they are allowed to participate in an economic game. The first move therefore signals better than anything else their expectations brought into the experiment—their interpretation of likely events as well as their own predispositions. After the first round, PGG subjects are known to demonstrate significant conformity bias (Carpenter 2004; Bardsley and Sausgruber 2005). Extreme contributors tend to move more towards the group average, though still maintaining a bias towards their initial action.

We classified those who invested their entire initial allocation to the group account as *Cooperators* (with a capital C). Those with who did not make any group investment at all, we classified as exploitative *Freeriders*. The rest (the vast majority of participants) we did not classify. We reasoned that if a person devotes their entire allocation to the group welfare, full cooperation is likely their default behaviour when interacting with strangers. Analogously, we assumed that people who do not make any effort to support their new group have a tendency to behave in an exploitative fashion, or at least not to trust others to cooperate.

We found that the variation across subject pools in the proportion of Cooperators is much greater than the variation in the proportion of Freeriders (Fig. 9.3): Levene's test $=6.71$, $p=0.01$; $MFREE\text{-}RIDERS=0.10$, $SD=0.05$; $MCOOPERATORS=0.20$, $SD=0.11$. We then ran correlations to determine whether there is a link between the proportion of cooperative types in a subject pool and the mean expenditure on punishment. The correlation between AP and the proportion of Cooperators ($r=0.35$, $p>0.05$) was not significant. Neither was the correlation between AP and Freeriders ($r=-0.18$, $p>0.05$) nor between the proportion of Freeriders and ASP ($r=-0.20$, $p>0.05$). In contrast, we found a strong anticorrelation between the proportion of Cooperators and ASP ($r=-0.62$, $p<0.01$; Fig. 9.4).

This means contrary to expectation that the variation between cultures may be primarily the difference between the probabilities of individuals playing an optimistic, cooperative strategy. Such behaviour may *inhibit* the expression of ASP even in regions/socio-economic contexts where we had hypothesised unexpected generosity served as a trigger—where it was likely to be viewed as a competitive or dominance-seeking act. Perhaps extreme cooperation signals ingroup affiliation. However, anticorrelation does not allow us to infer causation. It may be

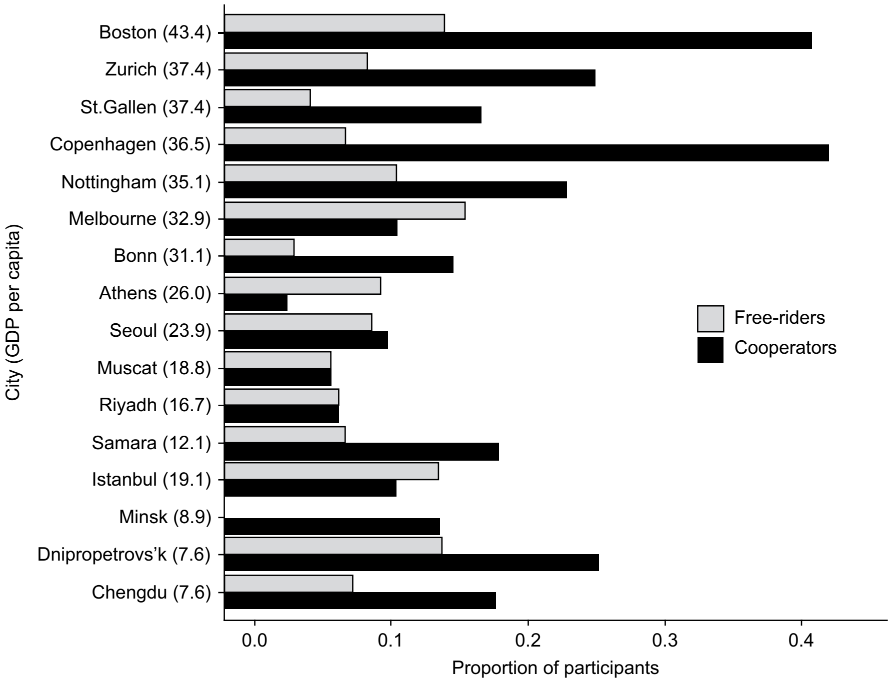

Fig. 9.3 Proportion of participants who contributed all (Cooperators) or nothing (Freeriders) by city. (Data from Herrmann et al. 2008a)

that expecting ASP inhibits reckless tendencies for cooperation. Our findings do however suggest more environmentally determined plasticity in the proportion of individuals with cooperative, rather than exploitative, predispositions. A multiple regression shows that a number of socio-economic factors predict the proportion of Cooperators but not Freeriders. Our analysis is the first to demonstrate that the distributions of extreme cooperative, but not uncooperative, tendencies differ across human populations.

9.4 Summary and Implications

In the previous sections, we documented our contributions to the behavioural anthropology of human economic decision-making, many of which derive from our taking an evolutionary approach and perspective. The assumption of this work is the standard one made in biology: that the seemingly bizarre behaviour of ASP must be a part of a behavioural strategy that is generally advantageous—or at least not disadvantageous—to people living in some cultural contexts, presumably the ones in which it is found. To briefly summarise our findings:

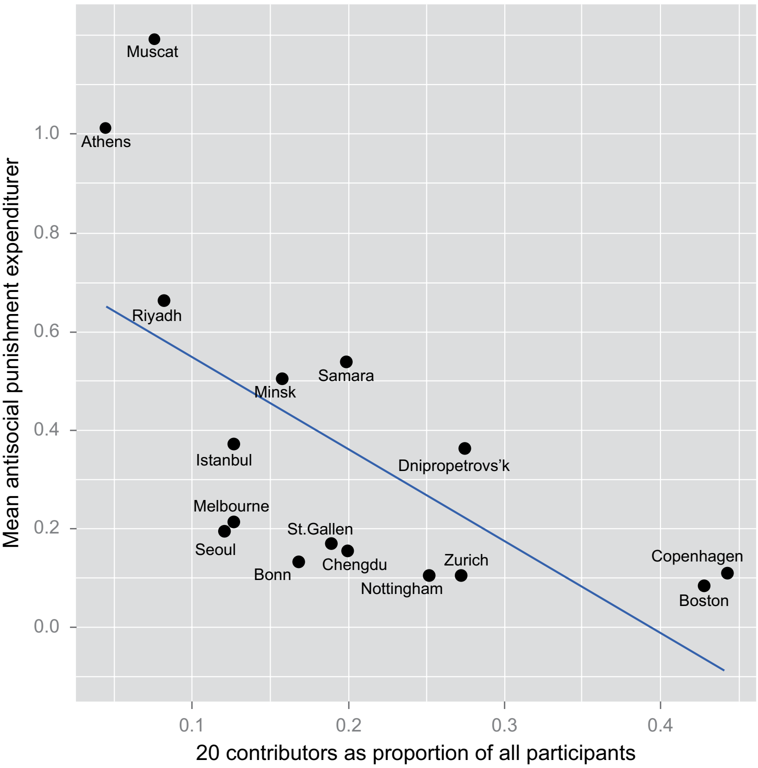

Fig. 9.4 Subject pools plotted by mean amount of ASP (y-axis) and the proportion of subjects who contributed all of their available resources (20 tokens) in the first round

- ASP has a disruptive more than a reliably down-regulating influence on cooperation. It does not reduce cooperation as reliably as AP increases it, but it does tend to alter investment behaviour, though again AP is even more likely to result in changed behaviour.
- Down regulating cooperation might make sense for an individual if that individual's wellbeing is determined more by local competition (e.g. who is most dominant in a household, village or business) than by global competition (e.g. which household, village or business does best).
- ASP seems to be expressed more frequently in games where members of a temporary artificial group do not by default expect others to be members of one of their real-life ingroups. With respect to the previous point, this implies that there is always *some* cohort of trusted individuals, and the question may be how large that cohort is by default. In Northern Europe (and Boston, the only US city surveyed here), the ingroup seems to encompass group sizes at least as large as a single university, while in Greece, Turkey, the Middle East and the former Soviet Union, it does not.
- Whatever the *default* level of ingroup assessment is, some manipulations might alter this. The only ones we could explore without performing human subject experi-

ments was the natural experiment of seeing how subjects respond to having someone in their group who contributes all or none of their resources to the public good. Interestingly, we have learnt here that having super-defectors in the group has no effect, but having super-cooperators in the group is correlated with a reduced level of ASP. This might mean that people inclined to ASP are impressed by such a clear expression of ingroup assessment and have some tendency to believe and adopt it. This hypothesis needs to be checked with further human-subject experiments.

9.4.1 Applications to Policy

This last point—that manipulations which increase the probability of ingroup assessment might also decrease levels of ASP and increase economic viability overall—is one of obvious potential, should experimentation bear it out. The one potential manipulation for which we have any data though may be difficult to replicate. Even if having group members who make extremely altruistic contributions does inhibit competitive tendencies rather than just covarying with such inhibition, the experimental context is highly unusual because of its transparency. All subjects know they have equal access to information and equal power under the authority of the experimenter. In a more realistic context, showing total economic commitment or some other signal of ingroup affiliation may be difficult to control, particularly by outsiders. There may, however, be other team-building exercises that would have at least local efficacy in facilitating negotiations.

Many people likely to read this chapter can recognise and identify with the ingroup assessment apparently made by subjects from Boston (Harvard) and the Northern European universities tested. Knowing someone else has chosen the same college or university as we have, particularly in the same or similar year, does indicate a likely similarity. An undergraduate degree is a significant investment—even where tuition is free, a degree requires 3–5 years of a person's life. For many of us, making similar investments at this scale is enough to incline us towards ingroup trust, but then we live in societies with a high rule of law (cf. Sect. 9.2). Understanding the social experience of those who cannot make this assumption about their colleagues requires effort for those who can. However, almost anyone will have had *some* experience of being in a situation where we were not sure everyone in the room was interested in collaborating for our mutual common good—where we have felt in danger of exploitation. In some cultures that feeling appears to extend even to the prestigious university campuses that Herrmann et al. (2008a) chose to study.[6] This might indicate that it could be unexpectedly challenging to achieve trust and therefore high levels of economic cooperation in other professional contexts as well as a university.

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[6] Because the initial studies were conducted at ETH, it was considered essential that representatives from other cultures were also drawn from top universities to increase comparability.

We must remember that in every society studied, ASP was practiced by some participants, but similarly in no society was it practiced by all. It may be that further experiments will identify in advance personality indicators for predisposition to ASP (e.g. Czibor and Bereczkei 2012). On the other hand, these may not exist. ASP may respond primarily to a combination of present and cultural context, combined with an element of stochasticity. However, even if we could determine who practices ASP, we have no idea of what the broader impact for a society would be if these individuals were excluded from positions of power or negotiation. As we mentioned, in some circumstances reducing group size or downregulating public investment may make economic sense; thus, those able to recognise this may be important members of a society or organisation.

We also do not know for sure that decreasing ASP and/or increasing cooperation would increase GDP. The causality could well be reversed—where individuals are affluent they can take more risks about ingroup inclusiveness. It seems likely though to be a situation of mutual feedback, and that if honest, transparent signals of mutuality of interest can be established, higher levels of both cooperation and economic performance could be established.

9.4.2 Conclusion

> To have received from one, to whom we think ourselves equal, greater benefits than there is hope to requite, disposeth to counterfeit love, but really secret hatred, and puts a man into the estate of a desperate debtor that, in declining the sight of his creditor, tacitly wishes him there where he might never see him more. For benefits oblige; and obligation is thraldom; and unrequitable obligation, perpetual thraldom; which is to one's equal, hateful. But to have received benefits from one whom we acknowledge for superior inclines to love; because the obligation is no new depression: and cheerful acceptation (which men call gratitude) is such an honour done to the obliger as is taken generally for retribution… (Hobbes 1651)

Our work has shown that Hobbes was amazingly prescient concerning the creation of public goods given that he wrote in the seventeenth century, but not entirely right. Our research indicates that ASP may indeed occur in contexts where other participants are not mutually acknowledged members of trusted group, and a gift from an anonymous peer may be met with suspicion or loathing. However, we have also seen that extreme generosity may in absence of other information be taken as an indication that in fact trust is merited and generosity should be accepted.

We have found that costly punishment is best understood as having impact not only on global economics but also on individual competition, and that the apparently maladaptive behaviour of antisocially punishing those more generous than ourselves may even in some contexts be a sensible response. When an actor's own wellbeing is (or at least appears to be) most determined by their relative dominance to their local neighbours, rather than to how well the neighbourhood performs as a whole, then it may be worth sacrificing immediate opportunities if longer-term benefits, e.g. in terms of social status result. For organisations that *are* more concerned about global than local good, the best course of action is probably to first promote the likelihood that the benefits of public goods are shared by those who invest in them, and second to promote transparency, so that all parties involved in investment decisions can be assured that their interests are protected.

Throughout this chapter, we have taken the perspective that the failure to find communal economic optima is fundamentally negative, since it means resources are wasted in conflict and all parties have less access to wealth and its associated well-being. Assuming this, the most directly applicable avenue for future research might be to discover how easily or quickly the social characteristics leading to this failure can be altered. Measures available could be either cognitive, such as increased transparency or reliability in the distribution of economic resources, or emotional, such as team building or other stage setting for triggering a state of emotional inclusiveness. If such measures work, a society's citizens and/or leaders could be trained to recognise, exploit or promote contexts where mutually advantageous outcomes were possible. However, it may be that for some societies such interventions would be impossible, impractical or unethical. Even in such cases, we could at least hope that the outcome of research in this area would still be beneficial. It would help us to at least identify, characterise and possibly come to understand cultures with such differences. This might be useful for selecting strategies in cross-party negotiations or in choosing between economic policy options or approaches to development.

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Part IV

Health & Diet Behaviours

Chapter 10
Socioeconomic Disparities in Health Behaviour: An Evolutionary Perspective

Gillian V. Pepper and Daniel Nettle

Abstract Socioeconomic disparities in health behaviour are a reliable finding across many societies. Individuals of lower socioeconomic status (SES) more frequently undertake behaviours detrimental to health (e.g. smoking) than those of higher SES. Despite a large volume of research on the subject, there is still no consensus on the causes of these disparities. In this chapter, we discuss nine categories of explanation which have been put forward in the social science literature. We then outline a complementary behavioural-ecological approach based on the idea that as extrinsic mortality increases, the payoff to investment in preventative health behaviour declines. We discuss how this evolutionary approach alters the interpretation of existing explanations, allowing us to reorganise the nine categories of explanation into three; ultimate, proximate and constraint based. We then discuss how this perspective can help to guide future research in public health.

10.1 Background and Aims

Socioeconomic status (SES) refers to ranking in a social and economic hierarchy and is usually measured by education, occupation, income or wealth (Pampel et al. 2010). SES disparities in health outcomes are a reliable finding. There are SES inequalities in life expectancy, in physical health and in mental health (Feinstein 1993; Adler and Ostrove 1999). Indeed, SES is so consistently linked with health outcomes that it has been classified as a fundamental cause of SES disparities (Link et al. 1995). There has been a large volume of research on the subject of SES differences in health. The website of the MacArthur Research Network on Socioeconomic Status and Health (http://www.macses.ucsf.edu/) lists nearly 700 publications between 1998 and 2009. These only represent a portion of the relevant literature. In

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this chapter, we focus on the literature regarding socioeconomic gradients within and between developed societies. The majority of the literature focuses on developed societies, because of the paradox of the persistence of health inequalities in modern welfare states (Mackenbach 2012). Despite this large volume of research, there is still no consensus on the causes of the gradient. However, what is clear is that a large part of the gradient is attributable to the health behaviours associated with SES (Mokdad et al. 2004; Stringhini et al. 2010). Why the people in society who face the most challenging life circumstances respond to them with behaviours which seem to exaggerate their problems is also an unresolved issue. In this chapter, we will briefly review some common explanations of SES differences in health behaviour. These explanations are often treated as competing hypotheses that must be tested against one another. None of them currently make use of an evolutionary adaptive framework. We will then review Nettle's (2010a) behavioural-ecological model of adaptive allocation of energy to preventative health behaviour. We will show how this evolutionary approach aids interpretation of the evidence and helps to reconcile the existing, seemingly competing, explanations. Our discussion emphasizes that an evolutionary framework can guide a more cohesive approach to future investigations of, and intervention policies aimed at, socioeconomic gradients in health behaviour.

10.2 SES Gradients in Health and Health Behaviour

Socioeconomic gradients in health outcomes within developed countries are well documented (e.g. Feinstein 1993; Adler and Ostrove 1999; Melchior et al. 2011). There are SES differences in life expectancy (Wilkinson 1992a, b; Phelan et al. 2010) and in healthy life expectancy (defined by the World Health Organization as "The average number of years that a person can expect to live in 'full health' by taking into account years lived in less than full health due to disease and/or injury"; Evans 2004; Liao et al. 1999; Crimmins and Saito 2001). Lower SES is associated with greater risk of a number of diseases. These include, but are not limited to: diabetes (Brennan et al. 2009), gastrointestinal diseases (Adler and Ostrove 1999; Levenstein and Kaplan 1998), tuberculosis (Cantwell et al. 1998), cardiovascular diseases (Laaksonen et al. 2008; Mobley et al. 2006) and arthritis (Sapolsky 2004; Kristenson et al. 2004). There are many mechanisms by which SES could influence health. However, this chapter will focus on socioeconomic disparities in health *behaviour*. We use the term health behaviour to encompass those activities which are beneficial for health. These could be either acts of omission (e.g. not smoking) or commission (e.g. getting health checks). Evidence suggests that SES differences in health behaviour account for a large portion of the gradient—up to half of it (e.g. Mokdad et al. 2004; Stringhini et al. 2010). People of lower SES more frequently exhibit risky health behaviours such as smoking and excessive drinking than those of higher SES (e.g. Pridemore et al. 2010; Harrell et al. 1998). Individuals of lower SES are also more likely to be obese, and less likely to take part in regular physical activity (e.g. McLaren 2007; Wardle et al. 2002). They are less likely to adhere to medication programmes and follow health-screening advice, even when these things are free (Barr et al. 2002; Goldman and Smith 2002; Qi et al. 2006). There is a higher incidence of teenage pregnancy (which is often conceptualised as a health issue) among lower-SES individuals and a higher rate of adverse birth outcomes (Johns 2010; Jewell et al. 2000; Adler and Ostrove 1999). There are even SES differences in the performance of basic self-protection behaviours, such as the use of seat belts (Colgan et al. 2004; Leigh 1990).

10.3 Classifying Potential Causes

A wide variety of explanations have been put forward for SES differences in health behaviours. They come from a diverse range of fields including epidemiology, sociology, behavioural economics and health psychology. It is challenging to review these, as they are so diverse and numerous, but Pampel et al. (2010) helpfully grouped them into nine main types. Here, we provide an abridged summary of their categories, which we have edited slightly for clarity. For full details and references, see Pampel et al. (2010). From here onwards, we shall refer to these categories of explanation as explanation types (ET) 1–9:

> *ET1. Deprivation and stress*: People of lower SES experience more stressful negative life events and use smoking, alcohol, drugs and junk food as buffers or self-medication against these.
>
> *ET2. Fewer benefits of health behaviours*: The benefits of health behaviours are lower for people of low SES because they are less likely to live to see the result. This is known as the Blaxter hypothesis (Blaxter 1997). Pampel et al. (2010) also classify the idea that people of lower SES have a preference for more immediate over more deferred rewards under this heading, but we henceforth classify this as belonging to the following category.
>
> *ET3. Latent traits*: Some third variable such as attraction to risk or to short-term gain explains individual differences in both SES attainment and health behaviours.
>
> *ET4. Class distinctions*: High-SES individuals adopt healthy behaviours in order to set themselves apart from lower-SES individuals.
>
> *ET5. Lack of knowledge*: People of lower SES lack knowledge that behaviours are bad for health.
>
> *ET6. Efficacy and agency*: Increasing education is associated with a greater sense of control and ability to exert choices, which allows people of higher SES to adopt more healthy behaviours.
>
> *ET7. Aids to health behaviour*: The resources needed to pursue a healthy lifestyle cost money that is less likely to be available to people of lower SES.
>
> *ET8. Community opportunities*: Lower-SES neighbourhoods lack health-supporting options such as shops selling healthy produce.
>
> *ET9. Social support and influence*: Lower-SES social networks are less likely to provide role models for healthy behaviours or sanctions against unhealthy ones.

Pampel et al. (2010) state that little has been done to systematically compare and contrast the categories of explanation which they reviewed. They say that, “this makes it difficult to offer an overarching framework that integrates or adjudicates between the various approaches”. This situation is not uncommon in the social sciences where, in the memorable words of Davis (1994), “while each article/book/course may be well crafted, they have little or nothing to do with each other.” We will argue that the use of an adaptive evolutionary framework helps clarify which of these diverse types of explanation are genuinely competing and which are different levels or components of the same overall story. To do so, we will now introduce Nettle’s (2010a) behavioural-ecological model of optimal health behaviour. We will then show how this can be applied to SES gradients in health behaviour to provide a useful big picture, clarifying the relationships among ET1–9, showing where the fundamental issues lie and helping to make novel predictions about how health behaviours can be changed.

10.4 Investment in Preventative Health Behaviour: A Behavioural-Ecological Model

Behavioural ecology is the study of behaviour from an adaptive evolutionary perspective; if many individuals living under some particular set of circumstances recurrently exhibit some suite of behaviours, then maybe those behaviours have an adaptive payoff under those circumstances (Davies et al. 2012; Nettle et al. 2013). Note that this does not mean assuming that the behaviours in question are under genetic control. Rather, natural selection on genes has endowed individuals with capacities for learning and plasticity that mean that they can find adaptive solutions to living in their local environments through non-genetic processes.

In the current case, it may seem counterintuitive to speak of adaptive payoffs. Survival is a central component of Darwinian fitness, and therefore, surely, investment in preventative health behaviours must always be adaptive. However, this ignores what is known in behavioural ecology as the principle of allocation. Individuals have finite energetic resources, and if they devote a unit of energy to one activity, they cannot be devoting that unit to something else. This leads us to the central behavioural-ecological idea of a trade-off. Investing a bit more in preventative health behaviour might always yield some improvement in survival chances, but there will come a point where the marginal benefit will not outweigh the cost, given that there are other things that could be done with the time and energy. Crucially, the terms of that trade-off might be different for people living under conditions of low versus high SES. They may have less time or money available to invest in health; or they may simply place a greater value on *other* things which they could invest time or money in. In addition to this, there may be short-term social benefits to unhealthy behaviours such as drinking, which outweigh the long-term repercussions for those living in lower-SES conditions, but not for those of higher SES. This will alter the terms of the trade off—especially if those of lower SES have less incentive to focus on the long term. The model, which we will go on to outline, demonstrates that this is likely to be the case.

Another central feature of behavioural ecology is the distinction between ultimate and proximate causes of behaviour (Mayr 1961; Tinbergen 1963). Ultimate explanations are about *why* a behaviour should occur in a given population and environment, in terms of the payoffs to that behaviour in that environment. Proximate explanations are about *how* that behaviour is generated, for example, the psychological or neural mechanisms involved. Importantly, these two different types of explanation are seen in behavioural ecology as complementary rather than competing. The distinction between ultimate and proximate explanations is not widely made in the social sciences, but it can be very useful. It will help us to make better sense of how ET1–9 relate to one another. We return to this below, but here we note that the model we outline is at the ultimate level. Ultimate explanations generally underdetermine the proximate mechanisms by which the adaptive behaviour is generated. This is true here; the model is compatible with several different hypotheses about the details of the psychology of investment in health behaviour.

Nettle's (2010a) model of optimal investment in health behaviour relies on three central axioms. (1) The first is that individuals experience some component of mortality which is *extrinsic,* meaning that it is not affected by decisions about health behaviour. The extrinsic mortality risk is the risk of mortality still faced by a person who has made all available investments in health behaviours. (2) The second is that investment in health behaviour is costly, in the sense that every unit of energy devoted to it is taken away from some other adaptively relevant activity or allocation. For example, time and energy devoted to health behaviour cannot be spent on activities such as gaining a mate, status or resources. (3) The third is that the effectiveness of health behaviour in reducing mortality risk is subject to diminishing returns. That is, the first unit of effort expended on preventative health behaviour has a slightly larger impact than the second unit, and so on. The model couples these axioms with the general principle of *optimization* (Parker and Maynard Smith 1990); that is, given these axioms, what would be the best thing for the individual to do if they were able to implement any behaviour?

The predictions in this case are very simple. As the risk of extrinsic mortality (the part people *cannot* do anything about) increases, the amount it is worth them investing in preventing the health risks they *can* do something about also decreases (Fig. 10.1a). This result is fairly intuitive. It seems quite pointless to make great effort to abstain from smoking if something you have no influence over is likely to kill you in the next few years anyway. Thus, people facing higher extrinsic mortality risks should reduce their allocated effort towards preventative health behaviour and reallocate their energy to other things. This in turn will increase their mortality risk, amplifying the initial difference in extrinsic mortality into a larger difference in total mortality (Fig. 10.1b). The model shows that even very small differences in extrinsic mortality can have quite large effects on optimal allocation to preventative health behaviour. This leads to a quite large final discrepancy in life expectancy. Note that although Nettle's model focuses on extrinsic mortality risk, the principle could also be extended to extrinsic morbidity risk. The payoff of health behaviour either in terms of healthy life expectancy or Darwinian fitness will be limited for individuals whose likelihood of suffering illness is beyond their control.

How can we apply this model to the SES gradient in health behaviour? Although we have pointed out that there are SES gradients in health behaviours, there is also

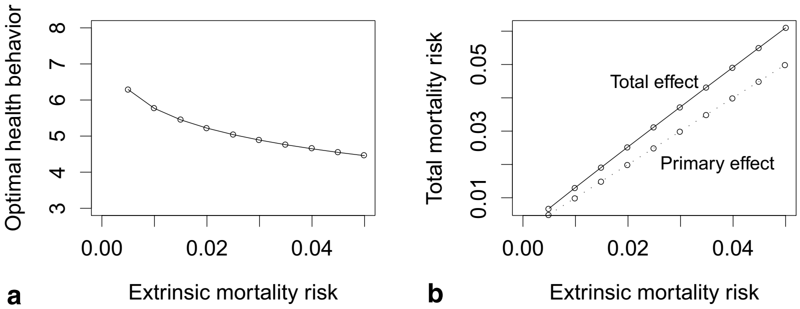

Fig. 10.1 Predictions from Nettle's (2010a) model. **a** As the risk of extrinsic mortality increases, the optimal investment in health behaviour (measured here on an arbitrary scale) decreases. **b** As the risk of extrinsic mortality goes up, the predicted total mortality rate goes up faster, through a combination of the primary effect of the extrinsic mortality and the secondary effect of people's response to it. (Reprinted from Nettle 2010a)

evidence that people of lower SES are exposed to more risks of dying from things which are beyond their behavioural control. For example, there are strong SES gradients in mortality due to homicide (e.g. Cubbin et al. 2000; Shaw et al. 2005), assault and other violent crimes (e.g. Leyland and Dundas 2010; Markowitz 2003). There are SES gradients in death due to traffic accidents and other unintentional injuries (e.g. Belon et al. 2012; Singh et al. 2012). There is also evidence that low-SES individuals are exposed to a greater number of environmental risk factors such as hazardous waste, toxins, air pollutants, ambient noise and crowded or unsafe residential and working environments (Evans and Kantrowitz 2002). Furthermore, evidence also suggests that people of lower SES do perceive that they are subject to a larger number of risks beyond their control (Wardle and Steptoe 2003). Although some of these risks might be reduced by avoidance behaviour (for example avoiding situations in which assault is likely), these sources of mortality are extrinsic with respect to the health behaviours which are typically examined in the literature (e.g. smoking, drinking or overeating). Furthermore, it may be that the best way to avoid these sources of mortality is simply to move away from deprived areas, a solution which is by definition unavailable to the poor. Lantz et al. (1998) demonstrated that, in a nationally representative US sample, mortality risk was greater for low-income groups than for middle-income groups, even after mortality due to all measured health behaviours was accounted for statistically. Thus, it seems reasonable to infer that people of low SES are indeed exposed to greater extrinsic mortality risk than their affluent peers (see also Lawlor et al. 2003). If we assume that the second and third axioms of the model hold, which is not unreasonable, then it actually makes adaptive sense for people of lower SES to be less concerned with preventing future health risks. The model predicts the most dramatic change in health behaviour with a small increment in extrinsic mortality where extrinsic mortality is low in absolute terms. This might help to explain why variation in health behaviour is more marked within developed nations that have low overall levels of extrinsic mortality than in those that have higher extrinsic mortality levels (e.g. Singh and Siahpush 2006; Cristia 2009).

The idea that lower SES is associated with greater exposure to extrinsic mortality might explain other traits besides health behaviours which are associated with SES. For example, individuals facing higher extrinsic mortality could be expected to place a greater value on the present than on the future. This is because high mortality risk increases the likelihood that one will not survive to reap future rewards, or to experience future penalties. There is evidence to support SES differences in time perspective and also to suggest that these may mediate SES differences in smoking cessation and in body mass index (Adams 2009a; Adams and White 2009; Adams and Nettle 2009).

People facing higher extrinsic mortality might also be expected to have children at a relatively young age (Low et al. 2008; Nettle 2010b). This is because when there is high mortality, waiting to have children increases the chance that one may not survive to have children at all. In addition, if one does survive to have children, having them sooner will improve the odds of surviving long enough to provide adequate parental care. We would also expect to see interactions between mortality risk and resource availability, because for those of high SES, waiting offers an opportunity to gather resources which can buffer against a risky environment and can be invested in children. However, this may not be possible for those of lower SES, no matter how long they wait. Again, the evidence supports this. There is a sharp SES gradient in age at first childbearing (e.g. Nettle 2010b, 2011).

Thus, we would predict that people should have an evolved sensitivity to cues of what level of extrinsic mortality they currently face, and that these cues should shift their behavioural allocations between current and future benefits. This prediction has led to the development of relevant psychological experiments. Griskevicius et al. (2011a) found that in a county-level analysis of data from the USA, income and violent crime (a factor contributing to mortality) were significant unique predictors of age at first reproduction. By comparison, levels of property crime (which do not contribute to mortality) did not predict age at first reproduction. Based on this finding, Griskevicius et al. went on to perform an experiment. Their participants either read a fake news article about a rise in random violent crimes or a control article about a stressful afternoon spent searching for keys. They found that individuals who reported a less wealthy upbringing expressed a desire to have children sooner (and a more positive attitude towards reproduction in general) when they had read the article about rises in violent crime. For participants who reported a wealthier upbringing, the same article produced a desire to further career and education at the cost of starting a family. Using a similar experimental method, Griskevicius et al. (2011b) found that individuals with low childhood SES who were exposed to the violent crime article subsequently chose smaller, sooner rewards over later, greater ones (they displayed greater future discounting) and were more likely to choose riskier options with larger rewards over smaller guaranteed rewards (they became more risk prone). Conversely, individuals of high childhood SES who read the violent crime article discounted future rewards less and became less risk prone.

These findings are a good example of how an evolutionary framework can guide investigations into the mechanisms underlying SES differences in behaviour.

10.5 How does the Adaptive Perspective alter our Understanding of Existing Explanations?

So far, we have summarized the nine categories of explanation for SES disparities in health behaviour put forward by Pampel et al. (2010), and outlined an adaptive explanation for SES disparities in health behaviour in terms of additional exposure to extrinsic mortality (Nettle 2010a). We have also made the distinction between proximate and ultimate levels of explanation. We will now go on to discuss how the adaptive approach and the proximate–ultimate distinction can change our perspective on ET1–9. There is in general no reason to think of evolutionary and non-evolutionary explanations as fundamentally at odds with one another. Indeed, formal evolutionary models may capture generalizations already made within social science (see Nettle et al. 2013 for discussion). The evolutionary perspective can provide a "big picture" overview on how the different parts of current knowledge interrelate.

In this light, we can divide ET1–9 into just three more inclusive groups (see Table 10.1). First, the contention that people of lower SES receive *fewer benefits of health behaviours for longevity* is an ultimate explanation, and is remarkably consilient with the extrinsic mortality model we have set out (see below). Second, several of the other explanations can be seen as different accounts of the proximate mechanisms by which reduced investment in preventative health behaviours is delivered. For example, *self-medication and stress, latent traits* such as time preference and feelings of *efficacy* could all be aspects of the proximate psychology that delivers a disinvestment in taking preventative action for the future exactly when extrinsic mortality is perceived to be high. *Social support, class distinctions* and *community opportunities* are also explanations of proximate mechanisms, but these focus more on how patterns of health behaviours are maintained over time in particular social groups through social learning and norms. They do not explain why exactly those social groups initiate exactly those patterns of behaviour in the first place.

Third, the only types of explanation which do not relate at all to the adaptive approach are *lack of knowledge of health risks* and *aids for healthy behaviours*. These amount to claims that people of lower SES are simply ignorant in their health behaviour decisions, or do not have the option of behaving differently, and we can therefore label them non-adaptive, or constraint-based, explanations.

10.6 Added Value of the Evolutionary Approach

We argued in Table 10.1 that many of the existing social science explanations (ET1–9) relate closely to the adaptive approach of Nettle (2010a) outlined above. So what, then, is the added value of taking an adaptive approach? Does it provide anything

Table 10.1 Pampel et al.'s (2010) nine types of explanation for SES disparities in health behaviour reclassified and reinterpreted from an adaptive perspective

Level of explanation	Pampel et al.'s explanation type (ET)	Interpretation in light of adaptive model
Ultimate	*Fewer benefits of health behaviours* (ET2)	Increasing extrinsic mortality reduces the adaptive benefits of healthy behaviour. This is an ultimate explanation because it explains *why* the behavioural response is adaptive
Proximate	*Deprivation and stress* (ET1)	Deprived environments may entail greater extrinsic mortality. This could act as a trigger for reduced investment in health. Features of low SES life may also trigger stress responses, which could lead to "self-medication" using food, tobacco or alcohol. These explanations are mechanistic because they explain *how* behaviours are triggered, but not *why* they exist. Our extrinsic mortality explanation explains why we should expect differences in health behaviour to correspond with deprivation
	Latent traits (ET3)	Latent traits arguments presume some third variable causes both SES and health behaviour. These are proximate explanations because they describe *how* latent traits might link SES and health behaviours, but not *why* there should be variation in that latent trait in the first place. Our extrinsic mortality explanation suggests that differences in factors such as time preference (triggered by cues associated with deprivation) could be a latent trait
	Class distinctions (ET4)	Once established, SES differences in health behaviour may be further perpetuated by class distinctions. This is a mechanistic explanation because it explains *how* behaviours are reinforced as class norms, but not *why* they become associated with class in the first place. Our extrinsic mortality model explains why we should expect class differences in health behaviour
	Efficacy and agency (ET6)	Explanations about efficacy and agency suggest that education enhances sense of control and thereby increases the tendency to seek out solutions to health problems. This is a mechanistic explanation, which describes *how* SES might influence health behaviour. The extrinsic mortality explanation suggests that SES differences in motivation towards health behaviour and feelings of control over health may produce an effect which looks a lot like SES differences in efficacy and agency

Table 10.1 (continued)

Level of explanation	Pampel et al.'s explanation type (ET)	Interpretation in light of adaptive model
	Community opportunities (ET8)	These arguments suggest that SES differences in health behaviour may be due to differences in community opportunities. This is a mechanistic explanation because it explains *how* behaviours are reinforced, but not *why* they become associated with SES in the first place. However, our extrinsic mortality explanation highlights the fact that community features such as safety may be particularly important in explaining SES differences in health behaviour
	Social support and influence (ET9)	Explanations about social support and influence suggest that social learning and peer support are important for the spread of health behaviours amongst low and high SES networks. These explanations are mechanistic, because they describe *how* behaviour spreads through social networks, but not *why* behaviours differ by SES in the first place. Our extrinsic mortality explanation explains why we should expect initial SES differences in health behaviour
Non-adaptive explanations (constraint based)	*Lack of knowledge* (ET5)	This is a non-adaptive explanation. A lack of knowledge about health risks could be a fundamental cause of SES differences in health behaviour. However, as we have discussed in the chapter, we have reason to believe that this cause contributes a limited amount to SES gradients in health behaviour. For example, it cannot explain the persistence of SES differences in smoking, when it is now compulsory to print messages such as "smoking kills" on cigarette packaging
	Aids for healthy behaviour (ET7)	This is also a non-adaptive explanation. A lack of ability to pay for health aids could be a fundamental cause of SES differences in health behaviour. However, this explanation cannot account for the fact that many of the poorest people have unhealthy habits, such as smoking and heavy drinking, which actually *cost* money

which was not already available? Here, we briefly discuss several ways in which we believe that developing an evolutionary model is useful:

1. For clarifying what explanations are competing and complementary
2. For deepening existing explanations
3. Because of the implications for public health interventions

1. **Clarification of What is Competing and What is Complementary**

The most useful merit of the adaptive approach is that it clarifies how the different parts of the story relate to one another. Pampel et al. discussed nine classes of explanation and stated that it was difficult to adjudicate or integrate between them. Our evolutionary approach suggests that there may not be nine, but only two, conflicting accounts to consider. The first is the non-adaptive or constraint account: People of lower SES make suboptimal choices about health behaviour through lack of information or options (ET5 and ET7). By suboptimal here, we mean choices that they would change if they had better information or options. The second are the adaptive accounts, both at the ultimate (ET2, our model) and proximate (ET1, 3, 4, 6, 8, 9) levels.

Evidence for the non-adaptive account is at best mixed, and it may depend which health behaviours are being considered. In the case of healthy eating, for example, it is possible to mount a convincing case that the healthiness of a diet is strongly influenced by how much money one can spend on it (Drewnowski and Specter 2004; Drewnowski et al. 2007). However, there are other cases where the evidence is in clear conflict with non-adaptive or constraint accounts. The simplest health protection behaviours (e.g. seat belt use) cost nothing and yet are less used by low-SES groups (Colgan et al. 2004; Leigh 1990). In addition, leading causes of the excess mortality in low-SES groups include tobacco and alcohol. Far from costing something to avoid, these habits are expensive to engage in. This suggests that SES gradients in health cannot be attributed solely to a lack of ability to purchase health.

Nor is lack of information likely to explain the gradient. Health warnings have been printed on cigarette packets for many years and in many countries. Since 2002, cigarettes sold in the EU countries have been obliged to display warnings such as “Smoking kills” and “Smoking seriously harms you and others around you” on at least 30 % of the front of the packaging and 40 % of the back (EU *Directive 2001/37/EC concerning the manufacture, presentation and sale of tobacco products*). Despite this, social gradients in smoking habits in the EU countries persist (Lader 2008; Buck and Frosini 2012). Indeed, evidence suggests that desire to quit and use of smoking cessation tools do not differ across social class, while quitting success does (Kotz and West 2009). This implies that the gradient may be created by differences in motivation toward healthy behaviour rather than by ignorance of the risks. This is supported by evidence regarding changes in health behaviours in the UK between 2003 and 2008. During this time period, there was extensive government investment in public health information campaigns. Buck and Frosini (2012) examined how four behaviours (smoking, excessive alcohol use, poor diet and low levels of physical activity) changed during this time. They found that high-SES individuals dramatically reduced their levels of unhealthy behaviour during the public health campaign period, while low-SES individuals did not. Receiving specific health information may have improved behaviour in individuals already motivated to invest in health, while failing to change behaviour in others. Thus, a key prediction of the lack of information hypothesis—that the gradient would disappear if everyone were given better information—is disconfirmed.

The major alternative to the non-adaptive account is something along the lines of the Blaxter hypothesis (ET2): People of lower SES invest less in their future health because the benefits of doing so are less for them than for people of higher SES. The behavioural-ecological model, by distinguishing analytically between extrinsic and intrinsic mortality and following through mathematics, provides a non-circular theoretical foundation for the Blaxter hypothesis. It also clarifies some anomalies with the existing economic models that have made similar arguments. For example, Cutler and Lleras-Muney (2006) suggest that individuals with better education may obtain greater incomes and therefore may expect to be happier in the future. They argue that this makes more educated individuals more likely to invest in protecting their future. But the same economic logic could be used to make exactly the opposite prediction (Pampel et al. 2010): High-earning individuals face greater opportunity costs in investing in time-consuming health behaviours (sleeping, exercising and preparing nutritious meals) than low-earning ones. Thus, without the fundamental distinction between extrinsic and intrinsic mortality as a foundation, it is hard to ground these intuitively plausible hypotheses in sound theory.

What of the remaining possibilities (ET1, 3, 4, 6, 8, 9)? We would argue that they constitute different claims about the proximate process by which an adaptively patterned disengagement from investment in the distant future under conditions suggestive of high extrinsic mortality might be delivered. As such, they do not conflict with ET2 at all, and they do not necessarily conflict with one another. Instead, we could think of them as different proximate pathways that might all contribute something, and to which studies might eventually be able to apportion different weights in terms of their centrality. Many or all of them could play a role, though, and indeed with most human behaviours, multiple mechanisms, both individual and social, are involved. Note that just because these are proximate mechanisms, they are not of lesser importance than ET2. On the contrary, as we shall discuss below, mechanisms that were adaptive over evolutionary time may not optimize personal or societal welfare today, and those who design interventions need to understand the proximate mechanisms as much as if not more than the ultimate shaping forces.

2. Deepening Explanations

The next major merit of the adaptive approach is that it deepens explanation. Many of the ET1–9 are likely to be correct, but provoke the immediate response, yes, but why should that be the case? For example, people of low SES may be more present-oriented or motivated by immediate payoffs (ET3); yes, but why? People of low SES may feel that they have less control over their futures (ET6); yes, but why do they feel that way? Low-SES communities may have norms of smoking (ET9) and even use these as identity markers (ET4); yes, but why are SES gradients in norms consistently established in the same direction across different populations, so that they become available for identity marking? In each of these cases, the proximate factor is crying out for integration into a deeper explanatory framework. In this framework, preference for immediate payoff or subjective lack of control are responses delivered by an evolved psychology attuned to cues of extrinsic mortality, delivering adaptively patterned shifts in behaviour, which then become propagated through social transmission.

A related point is that several things which are often taken as exogenous traits may in fact be psychological reactions to living in environments containing cues suggestive of high extrinsic mortality. For example, time preferences (relative valuation of present and future benefits) are often invoked in the health behaviour literature, and they are generally assumed to be stable individual differences of exogenous origin (e.g. Fuchs 1982; Kirby 2009). They are not typically viewed as psychological responses to environmental cues. However, within the framework we have outlined above, it is possible to view SES differences in time preference as part of an adaptive response to differential exposure to extrinsic mortality risk. This insight has guided the experiments we reviewed above, whereby participants changed their future discounting behaviour in response to cues to extrinsic mortality (Griskevicius et al. 2011b). From this perspective, explanations about "attraction to short-term gain", which Pampel et al. classed as latent traits, may in fact be responses to an ecology in which there are fewer benefits of health behaviours for both longevity and Darwinian fitness. This might also apply to efficacy and agency and to risk preferences.

The strongest evidence for this contention comes from experiments showing that these "traits" can in fact be manipulated over short timescales (Mishra (under review); Ermer et al. 2008; Callan et al. 2009; Wilson and Daly 2004). For example, Callan et al. (2009) investigated the impact of "just world threat" on future discounting. They exposed participants to a video in which a woman talks about her experience of living with HIV. Half of their participants were told that the woman had contracted HIV after having unprotected sex with someone she met at a friend of a friend's party. The other participants were told that the woman contracted HIV after she was in a car accident and was given a blood transfusion with infected blood. The authors deemed the latter scenario a just world threat, because the woman could be perceived as an innocent victim, who contracted HIV without having done anything to deserve it. The participants that were exposed to this just world threat subsequently discounted future rewards more steeply than those who were told that the woman contracted HIV after unprotected sex. Callan et al. interpreted this finding as a link between the need to believe in a just world, and the ability to delay gratification. However, our evolutionary framework offers an alternative interpretation: the just world threat scenario acted as a cue, to extrinsic mortality risk. In the scenario where the woman contracts HIV through unprotected sex, the decision about whether to have unprotected sex with a relative stranger is under her control. In the scenario where she contracts HIV from a blood transfusion, the situation is beyond her control. The mortality risk is extrinsic.

Further evidence that future discounting may change in response to cues to extrinsic mortality risk comes from Li et al. (2012). They investigated discounting in Chinese earthquake survivors in comparison with controls, who lived in similar towns, but had not recently experienced earthquakes. They found that the earthquake survivors discounted future rewards more steeply than the controls. They also measured event-related brain potentials and found group differences in the neural responses to the discounting task. The results of such experiments suggest that the latent traits which have been treated (either implicitly or explicitly) as stable individual differences may in fact be flexible responses to cues from the environment. This may account for the inconsistencies in findings regarding time preference and health behaviours (Becker and Mulligan 1997). If variables, such as future discounting, are treated as fixed individual traits, our conclusions can be quite different from those drawn when considering that they may be flexible responses to ecological factors.

3. Implications for Interventions

The adaptive perspective has potentially quite significant implications for the design of interventions. It argues that disinvestment in health behaviours represents a sensible response to living in certain types of environments, namely those rich in unavoidable danger. The corollary of this is that there is no reason to believe that giving people living in such environments more information about, say, the harms of smoking, is likely to make a dramatic difference to their behaviour. In fact, such information-giving can actually increase disparities in health behaviour when it is implemented across whole populations, exactly because the most affluent are most motivated to attend to the information and update their decisions using it, while the poorest have less incentive to do so (White et al. 2009; Capewell and Graham 2010).

An adaptive perspective naturally draws attention to broader structural-ecological parameters. Roughly speaking, it predicts that if the *extrinsic* dangers of deprived environments could be tackled, then the behaviours would more or less take care of themselves. That is, if societies reduce the relatively high rates of violence, the dangers of jobs and buildings, the differential exposure to accidents and toxins, etc. that beset deprived communities, then people in those communities would be more likely to be motivated to stop smoking. At the extreme, this kind of argument leads to an insupportably strong claim that no public health interventions aimed directly at health behaviour are worth carrying out, since all people are already assumed to be behaving adaptively anyway. The only action worth investing in is political action to improve socioeconomic conditions. Although we do recognize the force in this argument, we would not wish to go that far. We do however endorse the view that improving the socioeconomic environment is desirable and has a double yield; it is a good thing to do in its own right, and it will have a secondary benefit as people respond by looking after themselves better.

A more nuanced position would be the claim that the relatively low investment in preventative health behaviours seen in deprived communities is the result of adaptive *mechanisms,* while not always representing adaptive *behaviour*. That is, natural selection has sculpted psychological mechanisms which lead people to respond to conditions of high extrinsic mortality by becoming more present-oriented and investing less in their health. Although those mechanisms have on average been fitness enhancing over the millennia, it does not follow that every time they are engaged, particularly in modern environments, they improve the person's fitness, still less their wellbeing. It is important to understand what determines people's perceptions of mortality risk, especially if perceptions of mortality risk are inaccurate. For example, evidence suggests that media coverage tends to skew people's perceptions of the risk of death due to given causes (e.g. Frost et al. 1997). It is possible that some portrayals of health scares in the news might worsen health behaviours, rather than improving them. Furthermore, reducing perceptions of extrinsic mortality may help to improve health behaviours, thereby reducing the inequalities that result from SES disparities in behaviour. There is much scope for applied evolutionary research in this area.

Finally, an understanding of the significance of psychological mechanisms attuned to cues of extrinsic mortality suggests some counterintuitive routes for intervention. Whereas intuition tells us that the most effective way to change health behaviour is to alert people to the risks of death that they face (as in the word "kills" on cigarette packets), it could be that such messages activate the mental schema of *extrinsic* mortality, making some people, perhaps especially those who live in harsh environments, feel that they are going to die anyway, and so there might be little point in trying hard to quit. If this were confirmed, then a health message pointing out that social conditions are improving and life expectancy has never been longer, and so there is all to try for, might actually have more effect than a negative message. This is a simple prediction that calls for further observation and experimental research.

So to conclude, the evolutionary perspective can bring a great deal of added value to much debated questions in public health. Rather than adding another seemingly competing explanation to the mix, taking an adaptive approach to understanding health behaviours can help to unite explanations from a diverse range of literature. It can help to clarify our understanding of what explanations are competing and what are complementary. It can deepen existing explanations and it can shed new light on the success and failures of health interventions. Yes, there is still much work to be done, but the evolutionary perspective undoubtedly has a good deal to offer.

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Chapter 11
Nutrition in a Changing World: How Economic Growth Drives Chronic Diseases

Jonathan C. K. Wells

Abstract Many modernizing countries are characterized by a dual nutritional burden—the simultaneous presence of undernutrition and obesity within populations, households, or even individuals. The dual burden is a primary risk factor for the epidemic of chronic degenerative diseases affecting such populations, and may benefit from an evolutionary perspective. Evolving in environments of ecological instability, the genus *Homo* developed a complex life history profile with multiple "nodes of flexibility" whereby the magnitude and rate of growth are sensitive to diverse ecological stresses. Through such plasticity, preagricultural populations could tolerate ecological instability, through time-lagged physiological sensitivity to fluctuating energy availability. This plasticity now renders contemporary populations vulnerable to new sources of nutritional instability, emerging from the role played by capitalist economics in the global supply and distribution of food. Chronic diseases emerge when rapid economic growth elevates metabolic load (adiposity, high-energy diet, sedentary behavior) over short-time scales in the absence of complementary effects on homeostatic capacity. An evolutionary perspective emphasizes the sensitivity of human metabolism to politico-economic factors driving nutritional trends. Successful prevention of chronic diseases is unlikely to occur without efforts to alter the power structures that characterize the contemporary food-industrial complex, restoring individual agency over diet and activity behavior.

11.1 Introduction

Until recently, undernutrition and overnutrition were thought to derive from very different environmental pressures, involving contrasting behavioral and individual risk factors (Doak et al. 2000). Undernutrition has generally been attributed to factors beyond the individual's control, such as poverty or famine. In contrast, overweight and obesity have typically been assumed to derive in part from the individ-

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ual's voluntary behavior, often expressed in popular speech as "gluttony" or "sloth" (Prentice and Jebb 1995). Given these different etiological models, it might seem unlikely that undernutrition and overweight should have a similar epidemiological profile within populations.

In the 1990s, however, nutritional surveys in low- and middle-income countries began to reveal high levels of overweight among women, even though stunting and underweight were still common among children. First reported from Egypt (Khorshid and Galal 1995), subsequent studies confirmed this finding in southern Africa, Brazil, India, Russia, and China (Doak et al. 2000; Florencio et al. 2001; Griffiths and Bentley 2001; Steyn et al. 1998). In Cape Town, South Africa, both nutritional extremes were already apparent in children (Bourne et al. 1994) indicating that overweight could develop early in life in a population essentially still suffering from chronic undernutrition. This scenario was termed the "dual burden" of malnutrition (Doak et al. 2000).

The most likely explanation for the emergence of the double burden is a rapid transition in nutritional supply, driven by economic development. Such rapid change could expose individuals within a common environment to very different influences, depending on their socioeconomic position. This conclusion was supported, for example, by data from successive national family health surveys in India, conducted in 1992–1993, 1998–1999, and 2005–2006. Over this period, undernutrition remained widespread, but the prevalence of overweight and obesity increased systematically, especially in some high-status groups (International Institute for Population Sciences 1995; International Institute for Population Sciences and Macrointernational 2007; International Institute for Population Sciences and ORC Macro 2000).

More detailed investigation, however, demonstrates that undernutrition and overweight are not separate entities affecting very different sectors of a given population, but rather tend to overlap substantially in their distribution within populations. The two nutritional extremes can coexist not only within communities or households, but can also be discerned within individuals. In many populations, a proportion of individuals are both stunted and overweight (Fernald and Neufeld 2007; Popkin et al. 1996). These individuals have therefore first encountered undernutrition early in the life course, and then gained excess weight later in the life course.

The dual burden represents something of a paradox. Through the twentieth century, European populations underwent a profound upward secular trend in height, equivalent in many populations to an increase of between 10 and 20 cm (Cole 2000, 2003). Such secular trends were widely attributed to improvements in living conditions and dietary quality. Deaths from infectious diseases fell substantially, but deaths from chronic diseases (e.g., coronary heart disease, stroke) increased, in part because relatively more individuals were living into old age. Equivalent data from low- and middle-income countries suggest that although secular trends in stature may be occurring, they are accompanied by the rapid emergence of obesity (Misra and Khurana 2008). Why, when dietary energy supply increases and infectious disease risk begins to fall, do these populations become fatter rather than merely taller?

In order to address the dual burden of malnutrition, I argue that an evolutionary anthropological approach is essential. Such an approach can offer sophisticated explanations for the data, due in part to its capacity to address the trans-generational basis of phenotypic change. The contrasting effects of improved nutrition on height versus weight and adiposity suggest that different components of phenotype can respond at different rates to ecological stresses. The double burden appears to emerge when the lingering effects of malnutrition have yet to disappear even as the onset of overnutrition manifests. An evolutionary anthropological approach may therefore help to identify the primary risk factors and the optimal approach to reduce its prevalence. If such explanations are indeed more accurate than those provided by the conventional biomedical approach, then evolutionary anthropological approaches will also represent the appropriate basis for public health policies intended to resolve the dual burden.

11.2 The Double Burden and Chronic Diseases

The rapid emergence of the double burden of malnutrition in developing countries is a key factor in the accompanying emergence of chronic diseases, such as hypertension, stroke, type II diabetes, and cardiovascular disease (Misra and Khurana 2008). Although these diseases were previously considered “diseases of affluence”, primarily affecting industrialized countries, low- and middle-income countries now contribute the greatest share of the global burden of chronic diseases (Ezzati et al. 2002; Lopez et al. 2006).

Both poor growth in early life and overweight in later life increase the risk of these chronic diseases, as well as other adverse outcomes. The contribution of low birth weight to chronic diseases was first highlighted in the early 1990s by retrospective cohort studies in industrialized countries such as the UK, Finland, and Sweden (Barker 1998; Barker et al. 1990; Barker et al. 1993a, b; Barker et al. 1989; Eriksson et al. 2001; Leon et al. 1998). This finding has since been replicated in many populations, and is supported by experimental studies in rodents and primates (McMillen and Robinson 2005). The contribution of overweight and obesity to the same chronic diseases was already well established. Obesity is a key risk factor for type II diabetes, and is also strongly implicated in the etiology of hypertension and cardiovascular disease (Despres 2001; Reilly et al. 2003). Mechanistic studies have demonstrated that early undernutrition and later overweight increase chronic disease risk by increasing the prevalence of a range of biochemical or physiological risk factors (McMillen and Robinson 2005), many of which are grouped together under the label the “metabolic syndrome.”

More detailed studies have elucidated the life-course patterns of growth that underlie chronic disease risk, although the majority of current research addresses cohorts born in the mid-twentieth century in industrialized populations, and the findings may not necessarily apply to all populations. Particularly valuable work has examined the growth trajectories of those developing overt disease in Finland.

Compared to those who did not develop chronic diseases, those who did showed poorer growth in early life and excess weight gain during childhood (Barker et al. 2005; Forsen et al. 2000). Similar findings have been reported from India in relation to glucose intolerance, the early stages of diabetes (Bhargava et al. 2004).

To interpret the epidemiological findings linking poor early growth with adult chronic disease risk, Hales and Barker proposed the “thrifty phenotype” hypothesis, arguing that fetuses exposed to a constrained nutritional supply in utero reduce investment in some organs in order to protect others (Hales and Barker 1992). Such a hierarchical growth strategy could protect the vulnerable brain during its most sensitive period of development, at a cost of growth in other organs associated with metabolism. In the short term, this strategy would improve survival, but the long-term penalty would be a reduced ability to tolerate the homeostatic challenges imposed by a high-calorie diet and sedentary lifestyle, each of which perturbs cellular metabolism. This life-course hypothesis formally challenged the prevailing wisdom, that chronic diseases were essentially the product of genotype interacting with adult lifestyle.

While initial emphasis was directed to an increased chronic disease risk in low birth weight compared with normal birth weight individuals, the studies in fact repeatedly demonstrated an inverse dose–response association between birth weight and chronic disease risk that applied across the whole of the birth weight spectrum (Barker et al. 1989). Thus, with each unit increase in birth weight, the risk of adult chronic diseases fell, and this beneficial effect was apparent even in those above average in birth weight. This surprising finding suggested that “fetal malnutrition” was not in fact the primary factor influencing disease risk.

A related point is that the statistical association between birth weight and chronic disease risk appeared either only, or most strongly, if adjustment was made for current weight (Lucas et al. 1999). Thus, holding adult body size constant, chronic disease was increased in those born small. In turn, holding birth weight constant, chronic disease risk was increased in those who attained high body weight. These two factors interact, such that the highest risk of chronic diseases is found in those born small who become large. For example, in Swedish men, the penalty for low birth weight was greatest in those who became tall or obese (Leon et al. 1996).

These findings indicate that chronic disease risk is not a simple outcome of fetal undernutrition, but rather emerges through inconsistent patterns of weight gain through the life-course, resulting in disparity between size at birth and size during childhood or adulthood. One reason why such disparity might be so influential for adult health, as noted by Hales and Barker (1992), is that the majority of rounds of cell division are completed by the time of birth. This means that fetal life is the primary period of growth during which organ structural variability emerges; from infancy onwards, the body can become bigger and more adipose, but large increases in body size cannot be matched by equivalent growth of the vital organs.

I have built on the thrifty phenotype model to describe in more detail the physiological basis of the link between growth patterns and chronic disease risk (Wells 2009, 2011). A number of different metabolic parameters scale positively with size at birth, as shown in Fig. 11.1. Lung function, lean mass, kidney volume, and beta cell mass all show such an association. Collectively, I refer to such traits as “meta-

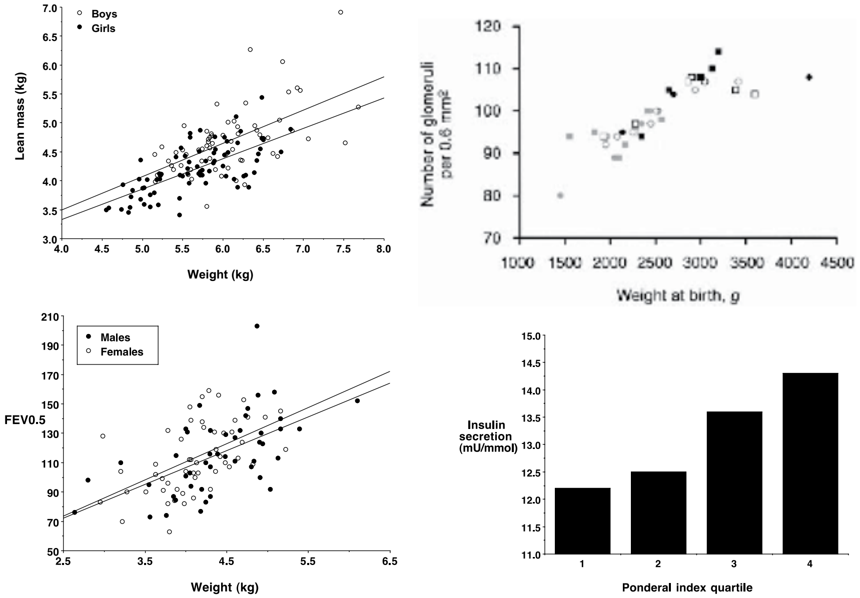

Fig. 11.1 Examples of homeostatic traits collectively termed "metabolic capacity" which scale positively with birth weight. (Reprinted from Wells 2011, with permission from Wiley)

bolic capacity," which acknowledges the role played by these organs in maintaining homeostasis. A larger birth weight therefore has long-term implications for metabolic capacity, since structural and functional properties of organs evident at birth tend to track on through the life-course.

In later life, the association between body size and chronic disease risk reverses, such that higher weight relative to height (body mass index, BMI) elevates the risk of hypertension, diabetes, and cardiovascular disease. BMI therefore manifests as an important component of metabolic load, by which I refer to traits that challenge the body's ability to maintain homeostasis. High BMI derives in large part from excess adipose tissue, and central abdominal adipose tissue is now understood to elevate cardiovascular risk by secreting inflammatory cytokines (Berg and Scherer 2005; Wisse 2004). Because organ growth during childhood tends to track growth in height through the influence of the insulin-like growth factor (IGF)1 axis, increases in BMI (weight increasing more than height) must inevitably increase the metabolic load on vital organs. Other components of metabolic load include a sedentary lifestyle and a diet high in lipid or refined carbohydrates. Each of these components of metabolic load challenges ongoing regulation of cellular fuel utilization (Corpeleijn et al. 2009; Storlien et al. 2004), elevating oxidative stress and inducing metabolic perturbations such as insulin resistance (Hoehn et al. 2009).

Chronic disease risk can then be modeled as a function of the ability of metabolic capacity to tolerate metabolic load (Wells 2009, 2011), as illustrated schematically in Fig. 11.2. Metabolic capacity might be indexed indirectly through birth weight, or more specifically through measurements of physiological function such as organ

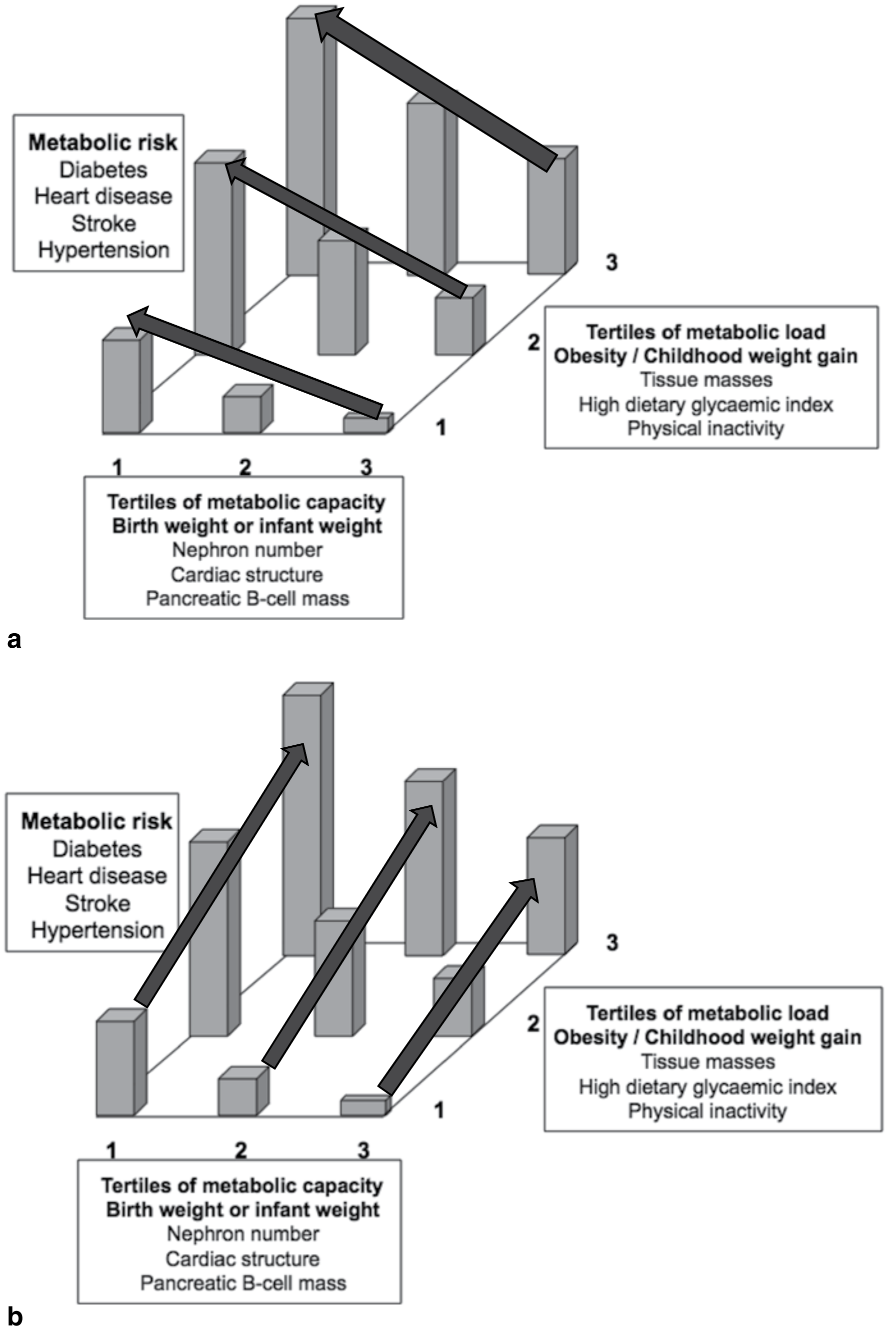

Fig. 11.2 Schematic diagram presenting chronic disease risk as a function of the interaction between metabolic load and metabolic capacity. **a** At any given metabolic load, disease risk increases with lower capacity. **b** At any given metabolic capacity, disease risk increases with increased load. The greatest disease risk therefore occurs in those with high low and low capacity, the scenario represented by the "dual burden of malnutrition." (Adapted and redrawn from Wells 2011, with permission from Wiley)

Table 11.1 Evidence for interactive associations of birth weight and later weight relative to height with indices of chronic disease risk

Risk factor or disease trait	Population	Reference
Blood pressure	Boys, 14–16 years, Philippines	Adair and Cole 2003
	Spanish adolescents, 10–18 years	Lurbe et al. 2009
	Systematic review	Huxley et al. 2000
Insulin resistance	Indian children	Bavdekar et al. 1999
	Finnish adults	Fagerberg et al. 2004
Glucose intolerance, diabetes	Indian adults[a]	Bhargava et al. 2004
	Finnish adults	Forsen et al. 2000
Serum cholesterol	Indian children	Bavdekar et al. 1999
	Swedish middle-aged adults	Fagerberg et al. 2004
Serum triglycerides	Swedish middle-aged adults	Fagerberg et al. 2004
C-reactive protein	Finnish young adults	Tzoulaki et al. 2008
Cardiovascular disease	Finnish adults	Barker et al. 2005
	Swedish adults	Leon et al. 1998
	Indian adults	Stein et al. 1996

[a] Weight measured in infancy rather than at birth

size by ultrasound. Metabolic load might be indexed by BMI, or more specifically by adipose tissue mass, dietary intake, and physical inactivity.

Numerous studies have now demonstrated interactive associations of birth weight and later BMI for chronic disease risk, as listed in Table 11.1. A relatively consistent pattern emerges, supporting the conceptual model presented in Fig. 11.2. Holding birth weight constant, chronic disease risk increases in relation to metabolic load. Holding metabolic load constant, chronic disease risk increases in inverse relation with birth weight. For example, in children from Pune, India, insulin resistance was greater in those with higher BMI at 8 years, and also in those born small (Bavdekar et al. 1999). The highest level of insulin resistance was found in those with high BMI at 8 years (high load) who were also born small (low capacity). This model therefore helps explain why the double burden of malnutrition in individuals represents a "fast track" to chronic degenerative diseases.

The capacity load model is a conceptual approach to chronic disease risk, intended to help integrate information across diverse populations and settings. In particular, it may help address ethnic variability in chronic disease risk. For example, South Asians are now understood to have an elevated chronic disease risk compared to most other populations, such that for a given BMI, South Asians are substantially more likely to develop type 2 diabetes or cardiovascular disease (Ehtisham et al. 2005; McKeigue 1996; Misra and Vikram 2004). Much of this elevated risk appears to derive from their relatively low birth weight (reduced metabolic capacity) acting in concert with an enhanced tendency to develop central abdominal adiposity (elevated metabolic load) later in life (Joglekar et al. 2007; Yajnik et al. 2003; Yajnik and Yudkin 2004), a trait which might arise through genetic or environmental mechanisms.

The capacity–load model offers a useful basis for attempting to understand the effect of secular trends nutrition on phenotype. Variability in fetal growth repre-

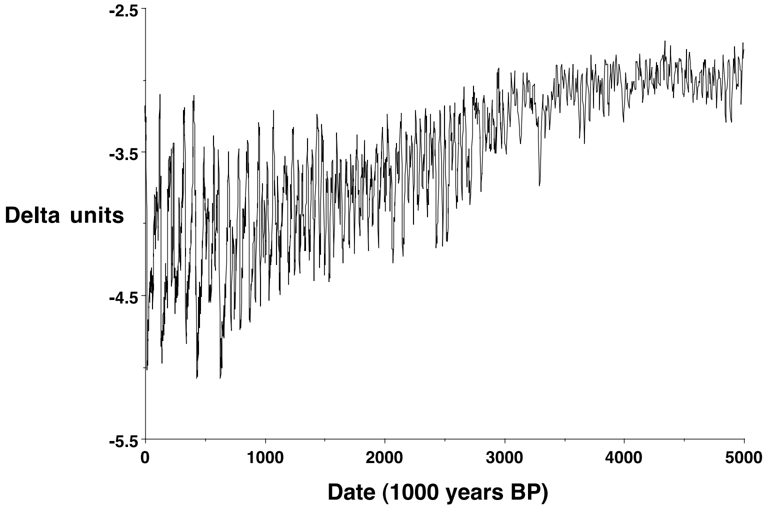

Fig. 11.3 Data on benthic 18-oxygen isotope concentrations, a proxy for global temperature. More negative delta ^{18}O units (isotopic enrichment relative to a standard water) indicate cooler temperature. Over the past 5 million years before present (BP), average temperature has fallen, but the magnitude of oscillations has also increased, indicating increasing ecological volatility. (Based on data from Lisiecki and Raymo 2005)

sents a component of developmental plasticity, which might be expected to represent some form of adaptation to environmental conditions. To understand why such developmental plasticity is so strongly associated with adverse outcomes in contemporary populations, the next section of this chapter considers why different components of human phenotype should be differentially sensitive to ecological conditions. We will then return to the issue of how nutritional trends elevate chronic disease risk.

11.3 Human Evolution and Stochastic Environments

Traditionally, human evolution was assumed to have occurred in the African savanna environment. The emergence of human characteristics—bipedal locomotion, large brain, pro-social behavior, cooperative breeding, and long life span—was assumed to have been favored by a hot, open, and dry environment (see Potts 1996, for review).

Increasingly, this savannah model is considered misleading (Potts 1996, 2012). A growing volume of palaeo-climate and palaeo-environmental evidence indicates that human evolution took place during an increasingly volatile ecological context. Figure 11.3 presents global 18-oxygen isotope data, a proxy for global temperature, over the past 5 million years (Lisiecki and Raymo 2005). Two significant trends can be discerned: First, there is a systematic fall in isotopic enrichment, indicating broad trends towards a cooler temperature. Beyond this, the plot shows increasing variability in temperature over time. This increasing palaeo-climate volatility equates to ecosystem instability. Potts has argued that the past 3 million years were characterized by substantial periods of climate stochasticity, and that the resulting ecological instability was the primary stress acting on hominin evolution (Potts 1996, 1998, 2012). Understanding how hominin biology adapted in response to ecological volatility is highly relevant to understanding how contemporary nutritional trends impact phenotype across generations.

Some of the climate trends can be attributed to irregularities in the Earth's orbit, known as Milankovitch cycles. These cycles introduce variability in the Earth's exposure to insolation, and hence in ecosystem productivity (Mayewski and White 2002). Such long-term cycles operate over tens of thousands of years, and might be expected to elicit adaptation by natural selection. Paradoxically, however, recent analyses of the human genome indicate a higher level of genetic unity in contemporary humans than in nonhuman ape species, despite human ethnic groups occupying a wide diversity of habitats (Kaessmann et al. 2001). Thus, genetic change may not be the primary way that human biology responds to long-term but local ecological trends (Wells and Stock 2007, 2011), and the most likely reason for this scenario is that ecological trends do not only comprise slow-period cycles but also much more rapid forms of stochasticity.

Building on Potts' work, I have recently discussed shorter-term climate cycles such as those currently manifesting as El Niño Southern Oscillation (ENSO) cycles (Wells 2012a). The current manifestation of ENSO may have existed only for a few thousand years; however, the palaeo-climate record indicates that some form of ENSO dates back several million years (Couper-Johnston 2000). ENSO cycles are driven by periodic temperature differentials across the Pacific Ocean, which promote irregular but frequent extreme droughts or floods in specific global regions (Glantz 2001). The biota of these regions is therefore subject to powerful selective pressures, favoring traits that allow such stochastic environments to be accommodated (Couper-Johnston 2000).

Traits such as cooperative breeding, slowed growth, and high adiposity have been proposed to represent adaptations to environments characterized by irregular but frequent extreme events (Wells 2012a). These events would destabilize energy supply and increase the risk of infant mortality, as is demonstrated in contemporary famines where mortality is greatest in the youngest and oldest of the population (Menken and Campbell 1992). Frequent exposure to extreme events would therefore favor a higher rate of reproduction, which is consistent with the shorter inter-birth intervals of humans compared to other apes (Galdikas and Wood 1990). However, producing offspring faster must inevitably increase the maternal reproductive energy burden. This increased demand appears to have been resolved by cooperative breeding, which distributes these energy costs across a pool of cooperating kin (Hrdy 2005, 2009). High levels of adiposity are also assumed to have been beneficial, enabling the maintenance of reproduction despite temporary shortfalls in energy supply (Wells 2010a). Finally, the slowed growth pattern of humans also

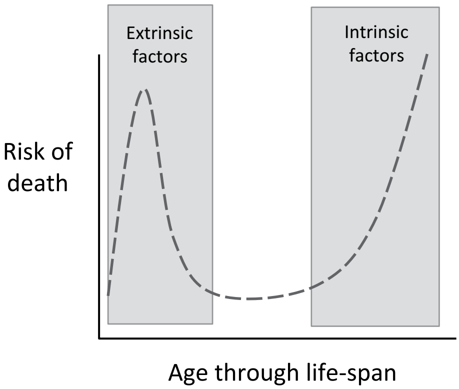

Fig. 11.4 Schematic diagram illustrating the typical human age pattern of mortality. In early life, mortality is dominated by extrinsic factors such as infectious disease. In later life, intrinsic factors increasingly dominate mortality risk, due to progressive deterioration of cellular function through the ageing process

contributes to the viability of cooperative breeding, by reducing the costs of each individual at any time point (Gurven and Walker 2006).

Importantly, this approach downplays the role of the encephalized brain in early *Homo* evolution (Hawkes 2006; Hrdy 2009; Wells 2012a). Rather, stochastic environments are assumed to have favored reorganization of human life history and the emergence of a suite of related metabolic adaptations that collectively enabled a faster rate of reproduction to counter the increased risk of delayed conception or infant mortality. Once those metabolic adaptations had evolved, they may have been instrumental in permitting substantial increases in brain size.

A key implication of this “ecological stochasticity” approach to human life history is that it offers a single explanation for several traits that appear to differentiate humans from other extant apes. In one sense, therefore, both slow growth and adiposity can be considered adaptive for our species overall. As discussed earlier in this chapter, however, on an individual basis the combination of reduced growth in early life and high adiposity in later life are fundamental to elevated chronic disease risk. What is it therefore that elicits maladaptive outcomes from putative adaptive processes?

While slow growth reduces each offspring’s demand for parental (or alloparental) care, it also necessarily increases the time lag between the primary period of plasticity and the subsequent exposure to selective pressures acting on reproductive fitness. The characteristic life-course pattern of human mortality risk is shown in Fig. 11.4. Early in life, mortality is dominated by extrinsic (external environmental) factors, in particular infectious diseases (Kelly 1995). Later in life, intrinsic factors (pertaining to age-associated deterioration in the physiological capacity for homeostasis) become more important. Metabolic capacity and load are unequally exposed to these two stresses, hence contrasting ecological conditions between early life and later life challenge overall homeostatic strategy. In other words, metabolic capacity and load are generated through contrasting adaptive processes, and hence respond to different nutritional cues.

11.4 Information Processing

While nutrition provides resources for growth, it can also be conceptualized as "information" about the external environment (Bateson 2001). The period of developmental plasticity is therefore a crucial period of information processing, during which the developing organism must select an appropriate trajectory of growth and maturation on the basis of imperfect information. This information derives primarily from nutritional supply, which is obtained via the placenta during fetal life and via lactation during the early months of infancy, mediated by energy expenditure.

Contrary to popular wisdom, early human development is substantially resistant to nutritional perturbation (Wells 2003). Studies of maternal nutritional supplementation during pregnancy, intended to promote fetal growth in chronically undernourished populations, reported relatively modest magnitudes of effect. A randomized controlled trial in the Gambia showed a mean increase in birth weight of 136 g, although if the analysis was restricted to the season of greatest energy stress, the mean effect was 201 g (Ceesay et al. 1997). Although this supplementation program was successful in reducing the prevalence of low birth weight, it also showed that a significant increase in maternal energy supply generated a very modest increase in offspring birth weight.

In the opposite direction, complementary findings are apparent from studies of the effects of maternal famine. Classic work from the "Dutch hunger winter" in the Second World War showed that a reduction in the total energy supply of ~60 % reduced offspring birth weight by ~300 g (Stein et al. 2004), equivalent to only ~9 % of average prewar birth weight in the same population. In the Leningrad siege in the same war, a birth weight reduction of ~500 g (Stanner and Yudkin 2001) still equated to a reduction of only ~14 % in birth weight. Thus, when mothers experience profound deficits in energy intake, they buffer this stress and expose their fetuses to a reduced dietary stress.

Both the supplementation studies and the famine studies therefore indicate that fetuses are substantially buffered from external ecological perturbations (Wells 2003). Such buffering is consistent with the "safe harbor hypothesis," which proposes that developing offspring are protected from ecological stresses during sensitive developmental periods (Shine 1978). Through such buffering, maternal phenotype can smooth out short-term ecological variability and provide a more integrated and reliable signal of nutritional supply to the offspring (Wells 2003; Kuzawa 2005).

Simple simulations demonstrate the value of maternal buffering of the offspring from ecological stochasticity. One way to maximize this effect is to increase the period during which maternal phenotype provides such buffering, i.e., through extending the duration of pregnancy and/or lactation. However, this benefit clearly comes at the cost of reducing total maternal fertility rate, as conception of the next offspring requires a marked shift from physiological investment in the current offspring. An alternative way to increase buffering of ecological conditions is to transmit experience across generations, i.e., to dampen current sensitivity by increasing sensitivity to matrilineal experience (Wells 2003; Kuzawa 2005). For example, the

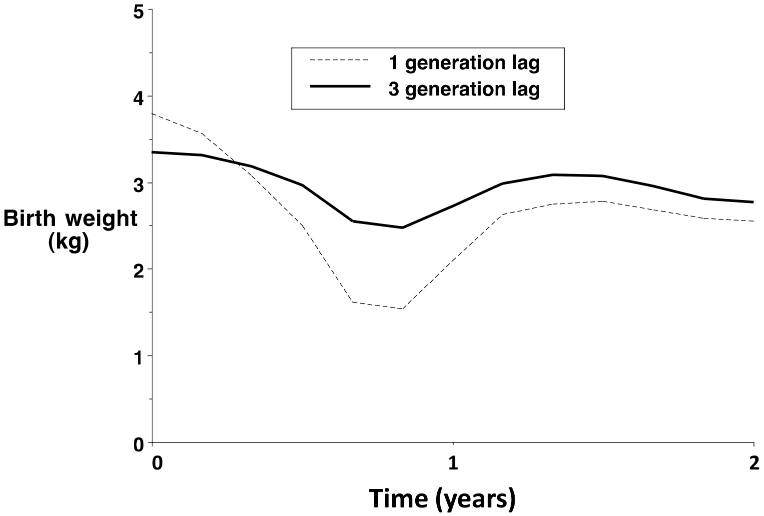

Fig. 11.5 Simple simulation illustrating how cumulative maternal buffering reduces the magnitude of penalties propagated to future generations following an extreme nutritional insult in the baseline generation. Here, maternal exposure to an El Nino famine event generates only a minor impact on the offspring's birth weight when there are counterbalancing grand-maternal and great-grandmaternal contributions to birth weight (3 generation lag), compared to the lack of such contributions (1 generation lag). (Based on an unpublished mathematical model)

effect of a current famine on fetal growth could be reduced if the mother did not herself experience famine during her own gestation, but enhanced if the mother did experience such famine. Figure 11.5 illustrates the consequences of such a multigenerational damping strategy where the population was exposed to an extreme ENSO event in generation one. Although this event induces a reduction in birth weight, the magnitude of that reduction is limited by maternal buffering. The multigenerational damping strategy therefore reduces the propagation of this adverse effect to subsequent generations.

Despite these clear benefits to the offspring of being buffered from short-term ecological stresses, complete buffering of offspring would be counterproductive, by preventing any adaptation to ecological trends over longer time periods. For example, ecogeographical associations have been reported between both physical and social ecological factors and birth weight (Wells 2010b; Wells and Cole 2002). A negative association is apparent between heat stress and birth weight, showing that birth weight is lower in hot environments. A positive association is apparent between per capita gross domestic product and birth weight, showing that birth weight is higher in more affluent populations. These trends clearly indicate that birth weight is sensitive to ecological conditions, with the impact transduced by maternal phenotype (Wells 2010b).

The information processing that occurs in early life derives from exposure to maternal phenotype (nutritional status, uterine volume, and pelvic dimensions), rather than direct exposure to the external environment. The influence of maternal buffering is lost however as the offspring is weaned and encounters ecological stresses directly. In this context, maternal phenotype can be seen to represent a protective buffer that is gradually withdrawn as the infant develops. In humans, this loss of physiological buffering begins at the time of delivery, when the offspring has completed only ~4 % of its developmental career, and is complete in traditional societies around 2–4 years of age, when breast-feeding is terminated. It is no coincidence that metabolic capacity develops during this brief window of maternal physiological buffering (Wells 2003). Metabolic capacity and load therefore develop in response to very different nutritional cues, making it easier to understand how sudden nutritional shifts over the course of development can perturb their relationship.

Following low birth weight, infants may undergo catch-up growth (Ong et al. 2000). In “natural conditions,” such catch-up may occur under the mediating maternal influence of lactation, but when complementary foods are introduced, this maternal constraint is lessened and growth rate can increase. At birth, low birth weight infants have low levels of the hormone IGF1, however, small infants respond to higher levels of nutrition by upregulating their IGF1 and insulin receptors (Muhlhausler et al. 2009), inducing rapid rates of growth which allow a partial recovery of the growth deficit achieved in utero. In experimental studies on nonhuman animals, other mechanisms facilitating catch-up growth include alterations in appetite, mediated by changes in brain leptin signaling (Coupe et al. 2010).

This maturational flexibility may be considered adaptive, allowing the pace of life history to respond to cues of ecological conditions, but it occurs too late to generate strong benefits on metabolic capacity. Offspring receiving lower maternal investment in fetal life should predict reduced longevity, and therefore divert subsequent investment towards reproduction (energy stores, faster growth; Wells 2012b). These are the same traits that contribute to metabolic load and chronic disease risk, hence catch-up growth introduces a disparity between load and capacity that favors reproduction at the expense of longevity. This trade-off may then be exacerbated by further ecological stresses.

11.5 Interaction of Nodes of Response and Perturbing Factors

While catch-up growth may provide short-term benefits, by improving the chance of infant survival (Victora et al. 2001), there are also potential physiological costs. Some of these costs may be relatively inflexible. In birds, for example, catch-up growth in early life was associated with elevated metabolic rate (implying energetic inefficiency) in adulthood (Criscuolo et al. 2008). Similar findings have been reported in rodents and humans (Qasem et al. 2012; Siervo et al. 2011). However, other long-term consequences of compensatory growth may depend on the quality of the environment that is encountered subsequently. The upregulation of IGF1 and insulin receptors makes tissues more sensitive to dietary composition in later life. For example, recent work has elucidated the impact of diets high in refined carbohydrate, which have been shown to perturb cellular metabolism.

Diets high in sucrose challenge normal glycemic regulation. Sucrose consists of 50% glucose and 50% fructose. Whereas glucose is metabolized through insulin regulation, fructose is converted to lipid in the liver (Bremer et al. 2012; Taubes 2008; Wells and Siervo 2011). The simultaneous release of lipid from fructose metabolism and insulin under the stimulation of glucose metabolism results in the insulin promoting rapid deposition of the lipid in adipose tissue. This metabolic activity temporarily reduces fuel availability to organ and muscle tissues, which provokes compensatory appetite elevation despite the high availability of fuel (Lustig 2006; Taubes 2008; Wells and Siervo 2011). Consistent with this model, randomized controlled trials have provided compelling evidence that diets high in sucrose promote fat accumulation around the organs and perturbations of blood lipid content (Le et al. 2009; Maersk et al. 2012). Until the origins of agriculture, humans are assumed to have consumed less carbohydrate and minimal amounts of sucrose, and would thus have metabolized glucose and fructose separately. Thus, modern sugar-rich diets represent a novel stress impacting human metabolism.

In turn, the sensitivity to this stress may be mediated by patterns of growth in early life. Upregulation of IGF1 and insulin during catch-up growth may increase susceptibility to ectopic fat deposition and altered lipid biochemistry (Wells 2012b). Contemporary middle-income populations may be becoming fatter rather than taller because although energy supply is increasing through economic development, it is also shifting in macronutrient composition, and becoming increasingly dominated by food products that perturb insulin metabolism (Bremer et al. 2012). Sedentary behavior likewise perturbs cellular fuel utilization, inducing oxidative stress and perturbing insulin metabolism (Corpeleijn et al. 2009; Storlien et al. 2004; Wells and Siervo 2011).

This perspective helps understand how the interaction between poor fetal growth, catch-up, and exposure to a rich diet or sedentary lifestyle later in life, as described in the double burden, may elevate chronic disease risk. Looking across a range of traits relevant to nutritional status, the data on secular trends indicate a variable speed of response. Each of height, BMI, and age at menarche can demonstrate an average change of a standard deviation score within a few decades, whereas birth weight changes more slowly, due in part to time-lagged maternal influences (Wells and Stock 2011). In a study of primates subjected to an improved nutritional supply over several generations, maternal weight increased but there was a time lag before offspring birth weight also began to increase (Price et al. 1999). The implications of this pattern of size change are shown in Fig. 11.6, where metabolic load can increase more rapidly across generations than can metabolic capacity, thereby increasing the risk of chronic diseases.

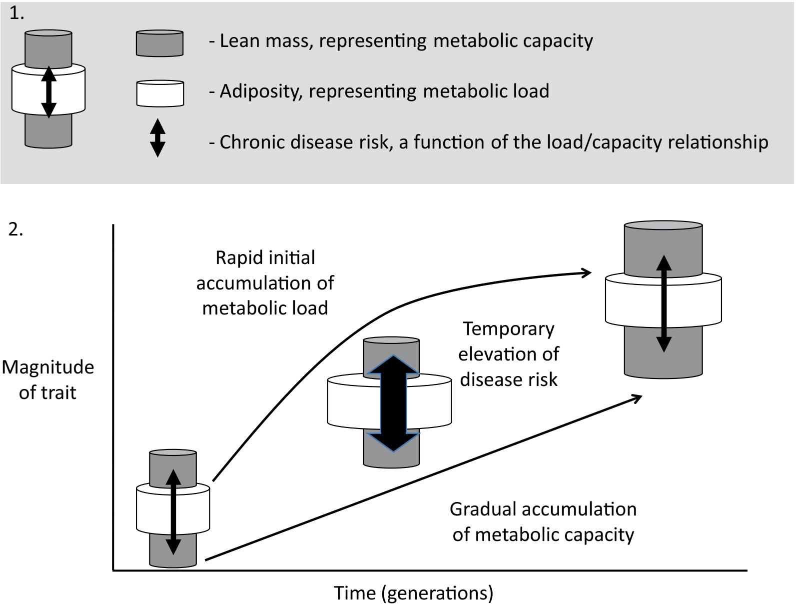

Fig. 11.6 Schematic diagram illustrating the differential ability of metabolic capacity and load to respond to changing nutritional conditions. Metabolic capacity represents a slow-response trait, whereas metabolic load represents a fast-response trait. Rapid shifts in nutritional supply may therefore exacerbate the load–capacity ratio, manifesting as the dual burden and predisposing to elevated chronic disease risk. (Reprinted from Wells and Stock 2011, with permission from Elsevier)

11.6 Economic Stresses and the Perturbation of Metabolic Signals

As discussed in previous sections of this chapter, the exposure of humans to nutritional shifts is nothing new, and can rather be assumed to have been a significant stress during human evolution. First, longer-term climatic trends have altered local ecosystems, as for example the global warming that occurred following the end of the last glacial period. Second, dietary shifts must also have occurred through migration between different ecosystems (Wells and Stock 2007, 2011). Third, dietary shifts may have arisen from human impacts on their own ecological niche, a process now described as “niche construction” (Odling-Smee et al. 2003). Such effects include ecosystem shifts through changing foraging patterns (Kelly 1995), and the emergence of agriculture (Cohen and Armelagos 1984).

What is different about more recent nutritional shifts is the extensive scale over which they act, their rapid timescale, and their power. The introduction of imperial plantation economies, the technology-derived ‘green revolution and finally the rapid expansion of global markets are all processes where large numbers of individuals have little agency, or ability to mitigate constraining influences. In particular, changes in the distribution of food are now arguably more important than changes in its availability or production.

Dietary shifts in the past few decades are frequently referred to as the "nutrition transition" (Popkin 2002; Popkin and Gordon-Larsen 2004), which describes not only shifts in the quality and quantity of dietary intake, but also concomitant changes in physical activity behavior which may decrease energy expenditure even as energy intake increases. The nutrition transition closely tracks economic development, and is an ongoing process in most lower- and middle-income countries, especially in urban populations but also in rural populations.

The nutrition transition is often portrayed as a relatively passive process diffusing through populations, yet in reality the transition is actively driven by a number of commercial companies, who aim to increase their global marketplace. Importantly, these commercial interests are not the first of their kind, but are following a previous wave of economic pressures more explicitly associated with European imperial activities (Wells 2012b).

What distinguishes these two eras of global economic influence is their contrasting mass influence on nutritional status. In the colonial era, imperial powers sought cheap labor to provide cheap raw materials for the consolidating industrial revolution. In this era, rural colonial populations were typically undernourished despite being required to contribute high levels of physical labor (Davis 2002). The nutritional status of large populations in many low- and middle-income countries still reflects this long-term economic stress. Many crops remain labor intensive, and the combination of low wages and high physical effort maintains populations in a state of chronic undernutrition.

Through the twentieth century, global economics followed the same transition as that already mapped out by Britain, the first country to industrialize. After a certain point, economic growth was hindered not by limits to production, but by limits to consumption and the size of the market (Hobsbawm 1968). More recent economic trends have been driven by the efforts of commercial companies to reinvent low- and middle-income populations as consumers, and the food industry is at the heart of these efforts. Initial efforts are targeted at rapidly growing urban populations, but rural populations are also increasingly exposed to new food products. Multinational corporations are increasingly building factories in low- and middle-income countries, and marketing new brands targeted at the local population. Extensive media campaigns aim to construct "new consumers," and inspired by these international efforts, local companies then follow the same course.

These marketing trends are the ultimate driving force behind the growing epidemics of chronic diseases: Focusing on the foods themselves is analogous to attributing malaria to the plasmodium, without acknowledging the role of the mosquito vector. Although health organizations are concerned about the impact of these economic trends on health, criticism remains muted because increased corporate activities manifest as increased economic growth. Manufactured foods provoke metabolic risk because of their perturbing effects on insulin dynamics (Bremer et al.

2012), and recent ecological analyses across large numbers of countries have shown associations between per capita sugar intake and the risk of type 2 diabetes, obesity, and hypertension (Basu et al. 2013; Siervo et al. 2014). An important mediating factor appears to be the relative amount of food imported into the country, indexing exposure to market forces (Basu et al. 2013; Wells 2013). Thus, simple models of increased energy intake and decreased energy expenditure fail to address the critical impact of metabolism-perturbing food products, and of marketing practices.

Fundamental to these dietary shifts is a loss of individual agency, so that individuals have reduced capacity to select their diet. This loss of agency is well accepted in relation to undernutrition, where individuals are typically well aware of the insufficiency of their diet but have inadequate opportunities to obtain or produce increased quantities or quality of foods. However, the same loss of agency is implicated in the development of overweight, where commercial practices are effective in driving consumers behavior, through manipulations of both metabolism (e.g., through the addition of addictive substances such as caffeine to sugar-sweetened drinks) and psychology (e.g., through slick marketing campaigns; Wells 2013). The key role played by loss of agency in the dual burden has been emphasized recently by studies of refugee populations. Long-term refugees are subject to major constraints on physical activity patterns, and also have minimal control over their food supply, as it is provided by international aid agencies. A study of Saharan refugees living in long-term camps in Algeria found high levels of both childhood stunting and overweight and obesity in adult women (Grijalva-Eternod et al. 2012).

11.7 Downward and Upward Trends

The contrasting trends in undernutrition and overweight are well illustrated by the anthropometric history of the Indian population, as shown in Fig. 11.7. Data on height can be reconstructed from skeletal evidence, historical records, and recent public health surveys. These data demonstrate that around 10,000 years ago, before the emergence of agriculture, male statue in the Indian population was around ~181 cm (Lukacs 2007). Around 4,000 years later, following the introduction of agriculture, male height had fallen by ~9 cm. By the late nineteenth century, male height had fallen by another ~9 cm, and averaged around ~163 m (Lukacs 2007). Over the long term, this equates to a height loss of ~0.2 cm per century. Likely predisposing factors were increasing population density, low dietary protein intake, and high infectious disease load.

Detailed longitudinal studies performed on 60 male populations between the late nineteenth and early twentieth centuries show a faster rate of decline, equivalent to 2 cm per century (Ganguly 1979). This rapid fall in height is likely to have arisen from the extreme famines, generated from the interaction between regular monsoon failure in the late nineteenth century and severe imperial economic policies, which substantially exacerbated the nutritional stress experienced by the Indian population (Davis 2002).

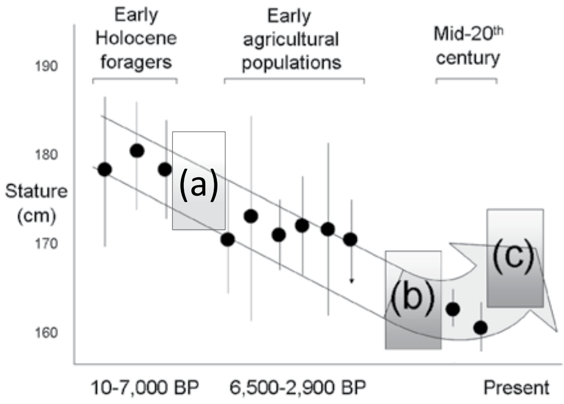

Fig. 11.7 The anthropometric history of Indian males, showing that preagricultural foragers were much taller than subsequent farmers (**a**), who in turn were much taller than colonial populations (**b**) in the twentieth century; modest upward secular trends have begun (**c**), but increases in weight and adiposity are much greater than those in height or birth weight. This population is therefore experiencing a major increase in prevalence of the dual burden. (Reprinted from Wells 2010b, with permission from Wiley)

Following rapid changes in the nutritional status of the Indian population, an upward secular trend in height is now occurring (Khanna and Kapoor 2004; Mamidi et al. 2011; Virani 2005), along with a modest increase in birth weight (Satpathy et al. 1990). However, the rates of these trends are much slower than those in body weight, BMI, and waist girth, reflecting higher levels of adipose tissue deposition.

The data from India therefore highlight the generic dilemma generated by the differential growth rates of specific parts of the body in response to antagonistic nutritional trends. The epidemic of overweight is associated with the efforts of diverse commercial companies targeting India as an "emerging market" nation, and driving trends in dietary intake and behavioral activity (Kuriyan et al. 2012; Wells 2013). Urban Indian populations are increasingly characterized by elevated metabolic load superimposed on nutritional constraint in early life, i.e., the double burden of malnutrition within individuals, and these traits are strongly implicated in the epidemics of diabetes and cardiovascular disease (Misra and Khurana 2008).

11.8 Policy Implications

In this chapter, chronic disease risk has been modeled as a function of two traits, metabolic capacity and load, which are each susceptible to ecological influences including those transduced by maternal phenotype. These traits can be reconceptualized as early growth variability, and adipose tissue biology, representing key

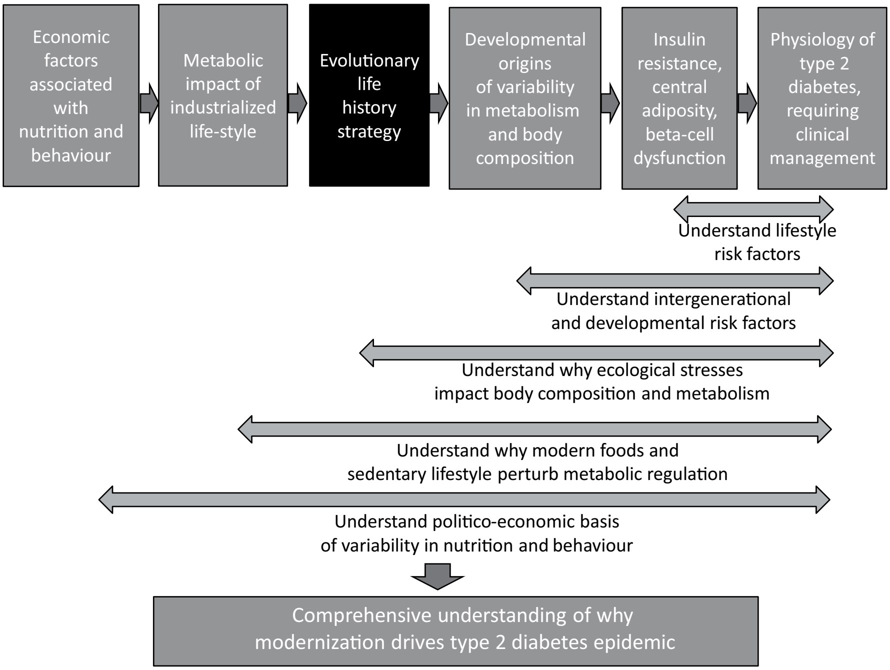

Fig. 11.8 Schematic diagram showing how an integrated set of approaches can combine to elucidate the association between economic modernization and the etiology of chronic diseases. Life-history theory plays a unique linking role, helping understand why the metabolic perturbations induced by obesogenic factors generate such complex effects on physiology, and why these effects might also vary between populations with different biological characteristics

components of life history plasticity. During human evolutionary history, such life-history plasticity is assumed to have favored resilience to stochastic environments, allowing survival during tough periods and rapid reproduction during good periods. In contemporary populations, the different rates at which metabolic capacity and load can respond to socio-ecological change results in the two traits being antagonistically influenced by global commercial activities impacting diet composition and food distribution, whereby metabolic load is rapidly elevated but metabolic capacity continues to reflect chronic undernutrition (Wells 2012b).

Paradoxically, public health efforts targeting undernutrition and overweight have very different bases. Whereas undernutrition is addressed by campaigns that aim to overcome individual-level constraints, overweight is addressed by encouraging individuals to “take responsibility” for dietary intakes and activity patterns that are in reality highly constrained by the operations of diverse commercial enterprises (Wells 2013). An evolutionary anthropological approach can play a key role in addressing this dilemma, by providing an integrated perspective that emphasizes how the metabolic effects of undernutrition and overweight each derive from a common life history strategy. Figure 11.8 illustrates a number of components of research, each aiming to improve our understanding of the role of modernization in the etiology of chronic disease risk. Life-history theory plays a key connecting role, helping understand how the metabolic perturbations induced by modern diets and sedentary lifestyle impact life history strategy through shifts in metabolism and body composition, thereby driving up chronic disease risk. Since metabolism is the "locus" of life-history allocation decisions, the effects of environmental perturbations are complex, and generate cascades of metabolic effects with diverse impacts on health and function.

This integrated approach highlights the severe impact of corporate capitalism on human health, and indicates that the global production and distribution of food merits radical reorganization in order to cut the global chronic disease burden. The global food industry is heavily implicated in the exponential growth in chronic diseases, because it is a key factor driving both the chronic poor nutritional status of "cheap labor" populations, and the epidemic of overweight of those targeted as "new consumers." However, governments have proven unwilling to regulate the activity of the food-industrial complex, because the production, distribution, and marketing of food commodities constitute a major component of economic growth. The dual burden of malnutrition reminds us that such economic growth comes at the profound cost of shortened longevity and increased chronic disease risk, especially in low- and middle-income populations.

Evolutionary public health policies can help address this through a trans-generational life-course approach. In the long term, sophisticated modeling is likely to prove essential for such efforts, addressing the way that life history "nodes of plasticity" interact with specific ecological factors. Already, however, the conceptual model discussed above suggests that efforts to constrain metabolic load may prove the most effective strategy for curbing chronic diseases, because of the relatively slow rate at which metabolic capacity can increase across generations. In particular, reduced exposure to obesogenic products such as sucrose may be most effective if targeted at populations at earlier stages of the nutrition transition, as above a certain threshold, the association of sucrose with obesity and hypertension plateaus (Siervo et al. 2014).

Above all, public health efforts to address chronic diseases are unlikely to be successful if they are not based on evolutionary principles. The adipose tissue that drives chronic disease risk when body weight is elevated is the same tissue that integrates growth and reproductive strategy while further funding immune function (Wells 2012c). Life-history theory represents a unique opportunity to introduce biology into economics, as both disciplines focus on the tailoring of strategy to environmental conditions.

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Chapter 12
The Evo–Eco Approach to Behaviour Change

Robert Aunger and Valerie Curtis

Abstract We introduce a new approach to behaviour change called 'Evo–Eco' because of its intellectual roots in evolutionary biology and ecological psychology. This approach is based on the inference that brains evolved to provide adaptive behavioural responses to rapidly changing or complex environmental conditions. From this foundation, we develop a model with three basic components: the *environment,* which presents some challenge or opportunity to the individual; the *brain,* which produces potential responses to that challenge; and the *body,* which engages in interactions with the environment (i.e. produces *behaviour*) that changes that environment. The behaviours of interest to behaviour-change professionals typically occur in particular settings, which can be seen as a context within which these basic components interact. We report how the approach has been used to develop public health programmes, as well as to make novel predictions about behavioural causes (i.e. placement of new target behaviours within a routine) which have proved to impact on the ability to change a behaviour. The Evo–Eco approach thus deserves to be used by public health workers and others to change behaviour.

12.1 Introduction

Behaviour change is a 'hot topic' in many fields with policymakers, marketers, educationalists, health promoters, business managers, sports psychologists, city planners and web designers all seeking to influence our behaviour. Behaviour change is often seen as 'hard'. However, humans are changing their behaviour all of the time. We have adopted life in megalopolises, fly from continent to continent, cope with multiple shifts in our jobs and participate in virtual social networks. Nowadays, children spend half their daily lives in school; currency—whether in coin or now online—provides the means for trade, and the Internet has changed many behaviours in communication, exchange and entertainment. In 1985, no one could

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telephone others when away from home; 25 years later, mobile phones are ubiquitous. People now take regular baths, give birth in hospitals, drive cars, wear glasses or hearing aids and use dishwashers. In fact, the rate of behaviour change may be becoming *faster* with time: Technology adoption curves are steeper than in the past; mobile phones have become endemic in only a few years, for example, whereas regular showering took many years to become popular (http://www.karlhartig.com/chart/techhouse.pdf).

Human psychology thus seems to be designed to produce changes in behaviour to match changes in the environment. Indeed, one reason why we have such large brains may be because humans have had to cope with particularly violent and shifting selection pressures as a result of environmental fluctuations, particularly over the past 10,000 years (Quartz 2001; Richerson and Boyd 2005; Potts 2012).

Behaviour is the quintessential adaptation of all animals. It can be defined as functional interaction between an animal and its environment, serving to keep bodies alive and reproducing through rapid, flexible self-propelled bodily movement (Aunger and Curtis, accepted; Millikan 2000; Plotkin 1988; Tinbergen 1963). Animals have had to succeed under conditions that require flexible behavioural responses, as their environments tend to fluctuate rapidly (Huey et al. 2003; Wcislo 1989; Wyles et al. 1983). They therefore evolved nervous systems and, later, brains that serve to detect and classify situations, to direct complex movements and to store information for later use (Aunger and Curtis, accepted; Freeman 1999; Sterelny 2003). Animals thus evolved nervous systems so as to be able to provide flexible behaviour in stochastic environments.

If the human brain evolved to produce behaviour in response to changes in the environment, then efforts to change behaviour would do well to begin by understanding the evolutionary history of behaviour and the brains that direct it, as well as the environments in which those brains evolved. Here, we introduce a new approach to behaviour change that is founded on this understanding of behaviour as a flexible, and mostly adaptive, response to changing environments and discuss some of its practical implications for public health.

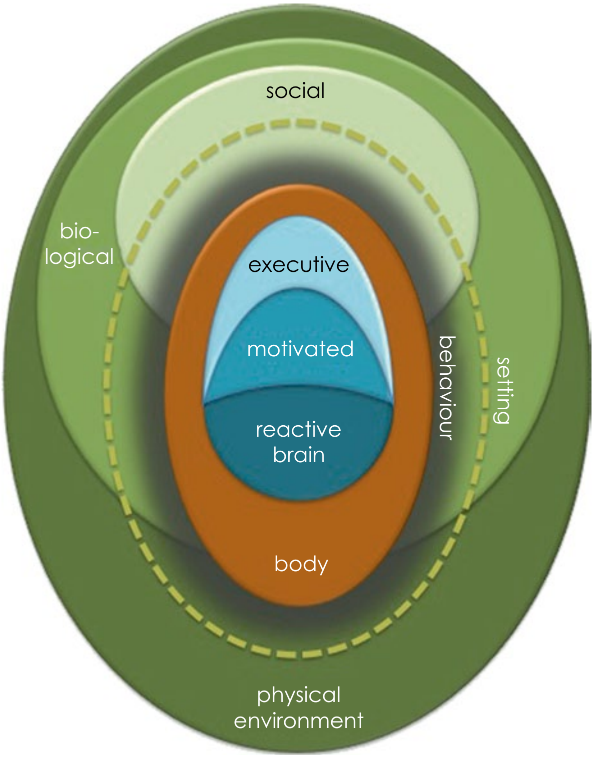
12.2 The Evo–Eco Approach

We have dubbed the new approach to behaviour change the ‘Evo–Eco approach’ for its dual origins in the evolutionary biology of behaviour and also in the ecological psychology of the 1950s (as we explain below). The approach can best be explained with reference to a simple model. Figure 12.1 schematises the basic components of behaviour. It has three fundamental elements:

The *environment,* which presents some challenge or opportunity to the individual

- The *brain,* which produces potential responses to that challenge
- The *body,* which produces *behaviour* that changes that environment

Fig. 12.1 The Evo–Eco model



The model depicts behaviour as a dynamic interaction between bodies and environments and situates brains, unsurprisingly, within bodies and bodies within an environment. The model, however, has more layers, breaking brains into three components for behaviour production and environments also into three categories. Later, we will break these divisions down even further (see Fig. 12.3), but we will begin by describing the evolution of the components of this simple model.

12.2.1 Brain

The first component of the model is the brain. The brain has a long evolutionary history over which it has acquired adaptations for controlling behaviour. Three levels of control have evolved in human brains, each of which can be isolated neuroscientifically (Daw et al. 2011; Daw et al. 2005; Dayan et al. 2006; Rolls 1999; Wunderlich et al. 2012). The earliest and simplest form of behavioural control system is the reactive brain. Following this came the motivational system, and to this was added a system for the executive control of behaviour.

The Reactive Brain The first type of control mechanism to have evolved came when early invertebrates such as jellyfish and worms appeared about 600 million years ago and remains characteristic of invertebrates. This was a system for simple reactions to environmental stimuli that represented opportunities or threats. Such brains operate by Pavlovian decision-making, which entails the release of species-specific approach and avoidance reactions in response to unconditioned or conditioned stimuli (i.e. reflexes; Pavlov 1927). So, for example, recognition of a potential food item would inspire approach among these early animal species, and contact with a toxin would inspire recoil (Abramson 1994; Krasne and Glanzman 1995).

Reactive brains can learn through classical conditioning, or acquiring associations between stimuli, or between stimuli and behavioural responses (Mackintosh 1985; Staddon 2003). This reactive-level learning is based on the Hebbian rule whereby neurons that ‘fire together, wire together’ (Hebb 1949), such that associations become stronger through experience. For example, in fear conditioning, an animal acquires avoidance responses to a previously neutral stimulus when it becomes paired with an aversive stimulus, such as a shock or loud noise. Reactive-level learning involves attaching a new link to an existing cluster of knowledge (e.g. faeces tastes awful, so the animal will recognize faeces next time as something to avoid). Such learning is also predictive in the sense that faeces will now be expected to taste bad whenever it comes into view, even without the experience—a learned aversion (Dayan et al. 2006). A special form of Pavlovian learning is ‘evolutionarily prepared’ learning mechanisms such as the Garcia effect, a mechanism that trains the body to avoid poisonous substances after only a single exposure, due to its significance for survival (Garcia and Koelling 1966). These acquired (rather than innate) automatisms are commonly called ‘habits’ (Lally et al. 2009; Ouellette and Wood 1998).

For the purposes of changing behaviour, innate automatisms are relatively inflexible, but can be triggered by the right cue (for example, a lactation response to the sound of a crying baby). Habits, on the other hand, can be trained; modifying them is an important task, since many of the daily behaviours that are important to public health, like tooth brushing, hygiene and food consumption, are acquired automatisms (Judah et al. 2012).

The Motivated Brain Above the reactive brain in the Evo–Eco schema is depicted a second brain system, the motivational system. This first appeared around 200 million years ago with mammals, whose characteristic adaptation is motivational control for goal achievement (Butler 2001; Northcutt and Kaas 1995; Streidter 2005; Willis 1985).

Motives are psychological adaptations for achieving particular kinds of goals. These goals are associated with carrying out elementary evolutionary tasks, such as finding food or a mate. Which motives a species can be expected to exhibit are determined by the niche in which the species lives, which in turn defines the evolutionary problems it must solve to flourish and reproduce (Aunger and Curtis 2008). All animals must find food, many must find a mate (if they depend on sexual reproduction), some must climb the social ladder of status (in species with social hierarchies). The means by which each of these niche-based tasks is achieved depend on the species’ evolutionary history (e.g. some species solve the food problem by scavenging, others by being predators). Evolutionary reasoning about how species including humans meet their particular needs and the available evidence suggests that humans have a total of 15 dissociable motives. These we have described and labelled as lust, comfort, fear, disgust, hunger, nurture, love, attract, affiliation, status, curiosity, hoard, create, play and justice (Aunger and Curtis 2013). Understanding the motives behind healthy and unhealthy behaviour provides a prime strategy to change behaviour. For example, disgust and status play a role in the decision to acquire a toilet (Jenkins and Curtis 2005), and nurture drives the responsive stimulation needed for a child to achieve its developmental potential (Engle et al. 2007). For health promoters, it is important to note that humans have not evolved a specific 'health' motive, as the conditions for good health are too general to have evolved a specific motivational system. Maintaining health is rather a life-long task underpinned by meeting the needs driven by the other motives.

The motivational system learns through what is known as 'operant conditioning' in the animal-learning literature, or reinforcement learning (i.e. 'learning by doing') in psychology (Sutton and Barto 1998). Mammals receive an internal reward for goal achievement (or not) through the midbrain dopaminergic system. The key feature of this system is the ability to derive an *expectation* of reward, such that the reward actually received for any action can be compared to this expectation to determine if the action is in fact leading towards the desired end state (Schultz 1998). Thus, progress towards goal achievement can be checked at various intervals, and alternative routes chosen if obstacles are encountered.

The Executive Brain When primates evolved about 65 million years ago, a third level of behavioural control arose. The executive control of behaviour (depicted as the top level of the brain in Fig. 12.1) is based on the ability to run through imagined scenarios of future outcomes. This deliberative level of decision-making entails search and evaluation of action options through a representation of the causal structure of the world (Tolman 1948). Some of the processing occurring at this level bubbles into consciousness, which is a limited 'theatre' in which memory and other information are pulled together for decision-making (Baars 1997). The executive brain employs declarative memory as a specialized mechanism for remembering the specifics of particular experiences, such as the license plate number of the car that just hit someone on the street or the name of a second cousin (Eichenbaum 2000; Tulving 1985). Declarative memory allows humans to develop highly specific scenarios based on detailed information and weigh up complex chains of potential future actions against one another. So, for example, plans can be made to make an appointment at a screening clinic because the value of the possible long-term health benefit is gauged as greater than the value of using the time to meet other needs. Much of current health promotion practice relies on the assumption that health-related behaviour is centrally driven by such rational decision-making and hence focuses on communicating the possible health benefits associated with particular courses of action. Our approach suggests that this will rarely be the most effective route to behaviour change.

This third level of behavioural control also has its own learning system, which employs meta-representation, or the ability to simulate complex situations, often symbolically (Sperber 2000). At this level, learning can happen vicariously, for example through sophisticated forms of social learning (i.e. learning by merely observing the actions of others), such as imitation (Bandura 1965). Also included here is reflective learning, in which various scenarios are simply imagined (rather than experienced) and new conclusions drawn—what might be simply called 'thinking' (Moon 2004). This process can also take place subconsciously through a process known as implicit learning (Seger 1994). In effect, these are various forms of 'learning without doing'.

The executive control system also stores representations of the self in declarative memory, giving individuals identities. Identity can play an important role in health behaviour; for example, changing one's identity to that of a non-smoker can assist with smoking cessation (Falomir and Invernizzi 1999; West et al. 2010). For behaviour change, another important form of declarative memory is social norms: People have ideas (based on experience) about what other people do (descriptive norms), and what other people think they should do (prescriptive norms), which can impact their own behaviour (through the motives to affiliate or to increase status). Communications that revise perceived norms of binge drinking behaviour downwards, for example, have been shown to lead to reductions in alcohol abuse in student populations (Perkins 2003).

All three behaviour control systems are operating all the time, in parallel. Having multiple decision-making systems allows the brain to make use of controllers with different advantages. The reactive system is best when there is a good expectation of a particular outcome (e.g. the consequences have been well established through previous trials). The motivated system is best for tracking needs and changing the environment to meet needs over a medium time horizon; the executive system enables the planning of behaviour over the medium to long term, sometimes overriding the other systems (Aunger and Curtis 2008).

With each behavioural control system operating in parallel, there must be psychological adaptations for selecting among options. There is some evidence that the three control systems are integrated (Daw et al. 2005; Daw and Shohamy 2008). For example, the control of behaviour can be shifted from one system to another through focal brain lesions, suggesting the coexistence of neurally distinct decision-making systems (Balleine and O'Dohety 2010; Dickinson and Balleine 2002).

The three levels of control can also interact in several ways. Of particular interest to the science of behaviour change is habit formation; a specialized mechanism that passes control from higher to lower levels of control through repeated experience (Dickinson 1985; Everitt and Robbins 2005; Yin and Knowlton 2006). Habit change can begin with a conscious decision to acquire a new behaviour, progress to motivated behaviour and, through continued reinforcement in regular environments, end up as a practised automatism. Over time, in stable environments, repeated behaviour leads to reduced errors, until these are eliminated, at which point the brain releases control to reactive level production (i.e. the response becomes habitual; Pasupathy and Miller 2005). This is Thorndike's 'law of effect' (Thorndike 1901).

In each step, repeated reinforcement leads to reducing the level of control necessary for continued behaviour production, ending up with fast-acting, automatic responses to environmental cues using a purely reactive level of control (Poldrack et al. 2005). Changing habits is a key challenge for behaviour of importance to public health, including daily hygiene, exercise, diet and compliance with medication. Efforts are being made to explore the determinants of habit formation and how daily behaviours such as hand-washing or fruit consumption can become learnt automatisms (Judah et al. 2012; Lally et al. 2009). For example, we are using smart home technology to test the prediction that provides a regular reward, such as a pleasant perfume in a soap, can lead to hand- washing becoming more automatic than it would be without that reward.

The fact that we have three different types of control systems can lead to problems. Reactive, affective and reflective systems have evolved to serve different ends and then been forced to work together. For example, an individual may use executive control to plan to avoid long-term health problems by not buying tempting food items, so as not to trigger the hunger motive, but then be unable to prevent an automated act of consumption when the plate of biscuits is offered by the well-meaning colleague.

This model of the brain, as composed of three types of behavioural control mechanisms with related adaptations in terms of learning, memory and action selection capabilities, is, of course, a major simplification. Each control system has had its own separate and joint evolutionary trajectory (Yin and Knowlton 2006) and the brain has other control functions; nevertheless, the three levels provide a useful heuristic for directing efforts at behaviour change.

12.2.2 Body

The second element of the Evo–Eco model is the body. This is our primary interface with the environment; we use it to modify our surroundings to better meet our needs. Several aspects of the body are important for behaviour change. First, everybody has a morphology, and this determines what sorts of movements can be undertaken. Each body morphology is unique and visible to others in the social group, which adds dimensions to one's identity—for example, ethnicity, gender and age group. Many behaviour-change programmes in public health target populations with specific combinations of these features (e.g. anti-smoking campaigns target young people before they develop the habit).

Second, the body produces physiological changes in response to signals from the brain that action is imminent. For example, arousal (increasing activation of the autonomic nervous and endocrine systems, leading to increased heart rate, blood pressure and sensory awareness in the presence of a threat or opportunity in preparation for action) is part of the physiological system. Arousal is also a way the body prepares for goal pursuit (Hull 1943; James 1884; Yerkes and Dodson 1908), so it can be considered an adaptation arising with mammals to 'energize' motivated action. More explicit use could perhaps be made of arousal in behaviour-change efforts, for example, fear arousal can change risk perception, leading people to avoid risky behaviours, such as dangerous sex in an era of HIV (Weinstein 1988; Witte and Allen 2000).

Third, the body also requires physical energy in order to move, which in turn requires mobilization of the body's chemical machinery. The body thus experiences an energy drain as a consequence of engaging in behaviour; against this, it must acquire resources. Reducing energy expenditure, to make healthy behaviour easy, is a classic tenet of health promotion practice—for example, in encouraging recycling or in using public transport (Hargreaves 2011). There is also evidence that cognitive energy depletion can lead to reduced ability to maintain executive control over behaviour, leading, for example, to overeating (Baumeister and Tierney 2012).

Fourth, the body enables people to engage subjectively with the environment through sensation. The senses provide the primary data from which the brain learns about its environment and the effectiveness of its behavioural strategies. Manipulating the sensory quality of experience is a potential route for behaviour change, more often employed in marketing than in public health, for example, the addition of sweeteners to toothpaste, the fresh smell to surface cleaners or the visual aesthetic of cigarette packaging. The recent addition of disgusting images of diseased organs to cigarette packs has helped counter their appeal (Cunningham 2009; Curtis 2013).

12.2.3 Environment

The third component of the Evo–Eco model is the environment. Though many models of behaviour mention environment, the term remains indistinct. In ecology, 'habitat', 'biome' and 'ecosystem' are all vague concepts, usually defined by the geographical features and ecological community of the species range (e.g. montane, aquatic, alpine). In evolution, the idea of a 'niche'—taken as a set of dimensions important to survival and reproduction—remains more abstract than useful for changing behaviour. At best, the niche has been conceptualized as a 'hyper-volume', or multidimensional space of resources such as nutrients, territory or mates used by organisms to satisfy biological needs (Hutchinson 1957).

For behaviour change, we need to be able to focus on the triggers of change that are extrinsic to people or 'outside'. We have therefore divided environmental phenomena into three types—physical, biological and social—as a function of how they influence behaviour (see Fig. 12.1). This division is supported by the sort of response that these different types of environment make to behaviour. The physical environment responds in simple Newtonian terms to behaviour: If you kick a stone, it flies away. An animal, on the other hand, can be strategic in its response, such as when a rabbit avoids being caught by a predator by scampering randomly away. Finally, a component of the social environment, another human being, can respond in elaborate ways to behaviour—for example, forming a life-long plan to get revenge for a perceived wrong. Because these responses occur in different ways, human brains should perceive and respond to physical, biological and social factors in the environment differently when producing behaviour.

Indeed, it appears that different kinds of deductions are commonly made with respect to physical, biological and social objects, as suggested by 'folk' physics, biology and sociology (Hirschfeld 2001; Medin and Atran 1998; Povinelli 2000; Ravenscroft 2010). Physical and biological objects tend to be distinguished in three ways: Physical objects are not expected to have internal motivation while biological objects are (Inagaki and Hatano 2006); biological objects are embedded in unique hierarchies (i.e. the 'tree of life') while artefacts can be in several hierarchies at once (Atran 1998); and animals do not have specific purposes (e.g. tigers are not 'for' anything in particular), but artefacts do (e.g. hammers are for hitting things; Greif et al. 2006). So, these three types of environment are real in folk psychological terms and hence should be distinguished in behavioural models.

Physical Environment What components of the physical environment are most important for behaviour? First of all, it is not commonly appreciated that most of the behaviours public health workers are interested in changing involve manipulating a technological object: condoms for safe sex, soap for hand-washing or seat belts and air bags to avoid injuries to car passengers. 'Focal' objects are key to the performance of many of the behaviours people seek to change. A key task for behaviour changers is thus to design or redesign objects so that they support healthy behaviour (for example, hypodermic needles that cannot be reused, or treated mosquito nets that are compatible with household cleaning routines).

A second aspect of the physical environment, 'infrastructure' is the consequence of long-term niche construction, conducted by human beings, often over generations. Infrastructure is the 'big stuff', often called the 'built environment'—things like a city's electricity grid, roads, skyscrapers or the World Wide Web. It consists of modified aspects of the environment which remain durable when used (Aunger 2010b). When infrastructure such as a public transport network or a hospital, for example, is designed appropriately, it can facilitate sustained changes in healthy behaviour, encouraging exercise or safe patient care (such as bathroom facilities to inhibit slipping while showering in nursing homes).

Biological Environment Our basic model of the biological environment is simple, as any animal only adopts a few types of behavioural relationships with other species. An animal can be a predator on other species, or the prey of a predator, or serve as a host or vector to pathogens, or be a pathogen, which predates on a host from the inside. Each of these relationships is associated with a specific psychological motive: Disgust helps us to avoid becoming a host (or vector) to parasites; hunger is designed to maximize our intake when we are acting as predators on plant and animal species; and fear (via the fight/flight/freeze mechanism) evolved for dealing with the proximity of predators (i.e. to help us avoid becoming prey). All of these relationships involve a biological agent passing through the body boundary in some form (e.g. by being eaten, taking a bite of the person or infecting the individual as host). Finally, species can play symbiotic roles, for example, as groomers or draft animals. Humans have complex funds of knowledge about the relevant behaviour and characteristics of the species in their environments to help them manage these relationships (Atran 1998; Medin and Atran 2004). The biological environment plays an important role in health-related behaviour, for example, by stimulating hand-washing when there is a perception that flu viruses are epidemic (Fleischman et al. 2011), offering foods containing plant toxins or leading us to interact with companion species that can transfer infections such as nematode worms and toxoplasmosis.

Social Environment The human social environment is more complex than the biological one. Mammals were the first large-bodied animal group to spend a significant proportion of their lifespan in the presence of conspecifics. However, early mammalian social groups remained largely egalitarian in nature. Primates were the first group in our evolutionary lineage to develop hierarchical societies, in which there is privileged access to resources, including mates (Boehm 1999; Mitani et al. 2012). Within these groups, there are particularly intense and long-lasting, dyadic interactions, which we call 'relationships' (e.g. mother and offspring).

Humans have developed social life to a unique degree. We depend on others to figure out how we should best achieve even everyday aims, being the species most adept at sophisticated forms of social learning, like imitation (Galef Jr and Laland 2005; Tomasello et al. 1993). We live in large groups composed of multiple subgroups. Institutions such as businesses, governments, sports clubs and religious organisations may meet in particular locations, with associated infrastructure, facilitating new kinds of cooperative outcomes. Each of these can be thought of as a network of individuals linked through particular kinds of relationships, in which each individual is playing a particular role, helping the organization achieve its ends. These networks can have regular kinds of structures (e.g. an organizational chart with a pyramidal shape) that dictate the ways in which it is possible to change roles within the organization. Institutional engineering represents a key strategy for changing behaviour. For example, doctors' job performance reviews can explicitly include hand hygiene compliance in efforts to reduce health-care-induced infections (Cherry et al. 2012).

Playing a given role in an organization, network or relationship can involve activation of a particular motive. For example, status maximization drives some people to become CEOs of businesses, while pleasure in skill development (the play motive) leads others to devote time to sport. Play has also been extended in primates from object play to social play, for learning the skills to interact with conspecifics effectively (Burghardt 2005). Affiliation is the motive to belong to a particular group, to share membership with others in a common goal (Aunger and Curtis 2013). The Evo–Eco model thus draws attention to the need to understand the structure of social relationships and the motives that underpin them. For example, we have shown that the nurture motive underlies much maternal caring behaviour including hygiene (Curtis et al. 2009), and Slutkin has shown the importance of understanding the status and justice motives in gang networks to prevent cycles of revenge violence (Chamberlin 2011).

Interactions

The three basic components of the Evo–Eco model interact in ways that are of importance to understanding how to change behaviour.

Behaviour First, brains compel bodies to move, which is a dynamic phenomenon. Because behaviour is ephemeral (unlike brains, bodies and environments), behaviour is represented in the Evo–Eco model as a cloud at the intersection of bodies and environments. Behaviour arises at a particular point in time, at a specific place, and then disappears again. For this reason, investigations of behaviour are often based on self-reports of past behaviour by those that have engaged in it, rather than on actual observation. However, this reliance on reporting can introduce major distortions in the understanding of what is really happening (Baumeister et al. 2007; Curtis et al. 1993). Since many health behaviours are normative and morally loaded or too automatic to be accurately recalled, it is important to document actual behaviour prior to development of behaviour-change campaigns rather than rely on self-report (see below).

Routines One implication of behavioural dynamism is that behaviours follow each other in a temporal stream. Behaviours often get chunked together in chains of actions that are statistically and functionally correlated in time and space (Ostlund et al. 2009; Simon 1974; Terrace 2001). The literature on routine behaviour divides behavioural chunks into routine, scene, event and action hierarchies (Schank and Abelson 1977). Figure 12.2 shows an example of a hierarchically organized behaviour stream concerning morning hygiene. This multilevel hierarchicalization helps behaviour to be controlled efficiently.

Chunking has implications for behaviour change. In a study of daily routines, we hypothesized that the order in which flossing is carried out with respect to tooth-brushing would influence its sustained adoption. Indeed, those participants in the study who flossed before tooth-brushing were less successful in forming a habit than those who carried it out afterwards, because tooth-care events seem to be chunked together, with brushing reliably cueing the next dental care event, flossing (Judah et al. 2012). We are currently investigating food hygiene in Nepal, oral rehydration solution preparation in Zambia and infant feeding in Indonesia with a view to finding ways of improving suboptimal behavioural routines.

Behaviour Settings Behaviour settings (shown as the dotted oval in Fig. 12.1) are one of the most important concepts in the Evo–Eco approach, where the components interact. The behaviour-setting concept derives from ecological psychology (Barker 1968). Settings can be thought of as networks of constraints on how animals can behave in specific situations. Settings first arose in the form of the stereotypical rituals and routines of animals—for example, with respect to mating or territorial disputes. Conventional signals and accentuated body movements become ritualized in such specific contexts to secure the best outcome (Krebs and Dawkins 1978; Maynard Smith and Harper 2003). These are situations of high risk and high reward in evolutionary terms; hence, appropriate behavioural responses have been strongly selected.

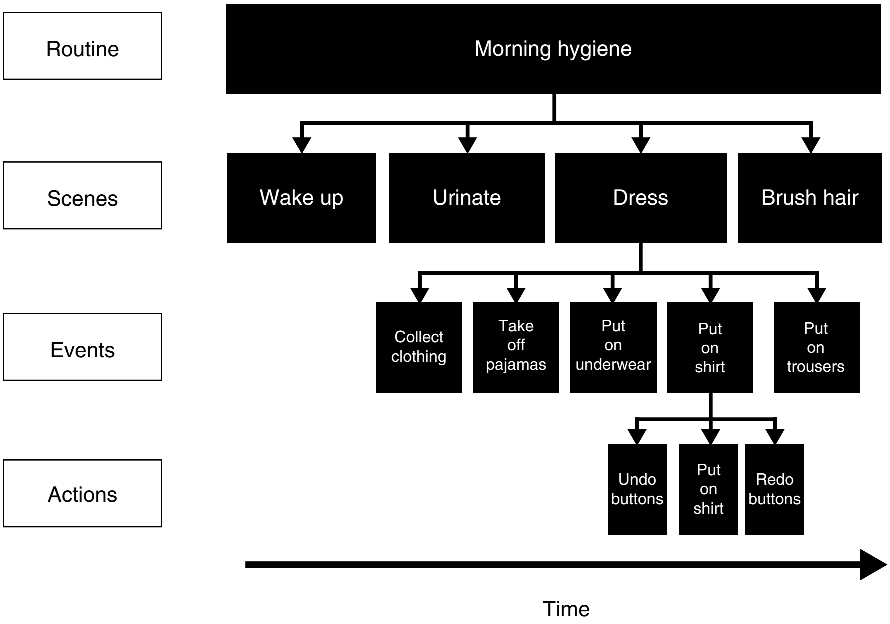


Fig. 12.2 A hierarchical behaviour routine

Most animals, from ants to lizards to primates, have daily routines in which they choose the same places and times to conduct a particular behaviour (e.g. feeding, getting water, marking territorial boundaries, resting, sheltering), day after day (Lorenz 1950; Serruya and Eilam 1996; Tinbergen 1963). Since reinforcement learning results in optimal behavioural choices over time, as long as conditions remain essentially the same, the same options should be chosen, and the same behaviours observed—hence the high degree of stereotypy in many animal behaviours. Behavioural rigidity—such as the preference to engage in specific acts at particular places and to take familiar routes between these places—is adaptive because it allows faster performance and enables attention to be directed to potentially varying aspects of the environment, such as the presence of predators (Barlow 1977; Boyer and Lienard 2006; Eilam et al. 2006; Young 1988).

Humans have elaborate behavioural settings, thanks to our ability to play particular roles, using particular objects, in particular physical and social environments. For example, we may produce stereotypical sequences of behaviour (i.e. routines) in a particular type of infrastructure (e.g. a church) using particular focal objects (e.g. a Bible), with people playing complementary roles (e.g. choristers, parishioners, lay leaders). This can be due in part to humans' tendency to 'over-imitate', or copy the most detailed, even non-functional aspects of other's behaviour (Lyons et al. 2007). People may (often simultaneously) enter into an implicit contract to complete the execution of a particular setting, such as a church service, school class, shopping trip, group celebration or private routine. Each participant plays a particular role within the setting, and if one individual behaves in a way that disrupts the setting, for example, by interrupting a wedding ceremony, others may feel that they have a licence to 'correct' them (e.g. by 'shushing' them or ejecting them from the scene). Hence, settings have a large degree of influence over the behaviours that most individuals exhibit in most social contexts. The ecological psychologist Roger Barker identified the powerful regulatory pressures that dictate behaviour in settings by collecting thousands of hours of observations and showing that behaviour within settings was 90 % predictable, if one knew only the physical and social context and the role an individual played (Schoggen 1989).

In social settings, this means that people performing their roles can help train others to perform theirs more appropriately—in effect, socially reinforced behaviour change. We have added 'Eco' to our Evo model in honour of Barker's important, but now largely forgotten, work on the ecologically determined psychology of everyday human behaviour (Barker and Schoggen 1973). Such regulatory mechanisms can be discovered by observing them in action. Settings are key to most health-related behaviours, for example, by determining when smoking is, or is not, allowed, by providing stereotypical rules for mealtimes, for ritualized ablutions and for patient–health-care worker interactions.

A further insightful contribution from Barker to the topic of behaviour change is the concept of 'synomorphy'. (A related notion is that of environmental 'affordance' (Gibson 1979). However, it is not as specific, nor part of as powerful an 'ecology of ideas', as the synomorphy notion developed by the Barker school.) Barker proposed that objects and infrastructure involved in settings often have design features that invite or dictate the performance of certain kinds of behaviour (Barker 1968; Gibson 1979). Synomorphies are adaptive kinds of 'fit' between environment, brain and body. For example, a bar of soap has a number of features that enable it to remove dirt from hands. It is about the size of a hand so it can be readily picked up and rubbed; it is solid, so that it will last a long time, yet when wet, bits are left on the hand, and further friction will cause the bits of soap to foam, providing transport of dirt from the hand when washed off under a flow of water. From the perspective of behaviour change, it could almost be said that the object dictates the behaviour, and hence attention must be paid to the design of the focal objects involved in the target behaviours.

In Fig. 12.3, we have added the additional components that we have discussed in this section to the basic model.

12.3 Comparison to Alternative Approaches

The Evo–Eco approach represents a powerful new way of thinking about behaviour and should have an impact on how interventions to change behaviour are formulated. It represents a major departure from the current dominant models of behaviour change—such as the theory of planned behaviour (Fishbein and Ajzen 2010) and health action process approach (Schwarzer 2008), in health psychology, and the 'heuristics and biases' approach in behavioural economics, based on deviations

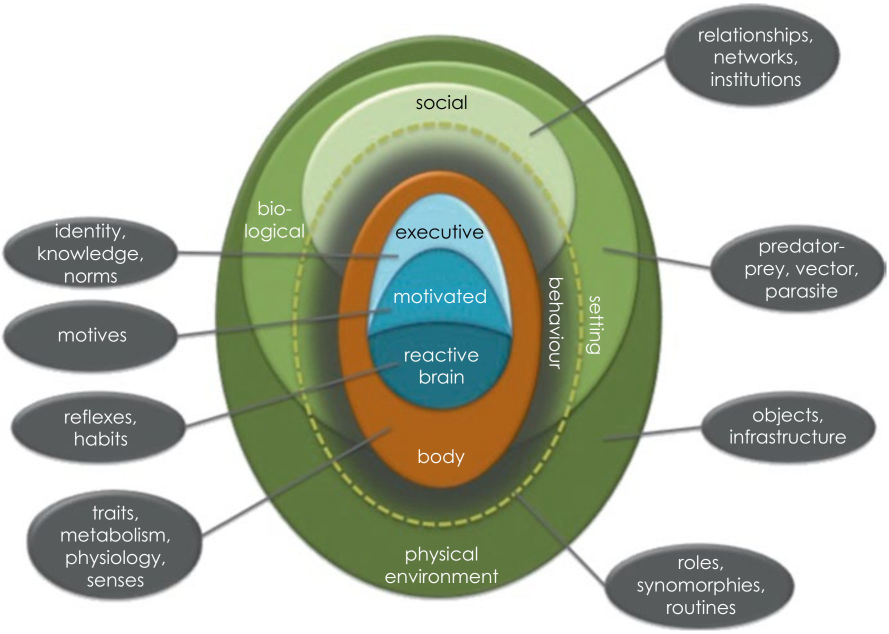


Fig. 12.3 The ‘exploded’ Evo–Eco model (with subcomponents)

from rational choice theory (von Neumann and Morgenstern 1944). (A few alternative models are available, primarily the social ecology approach (Stokols 1992), diffusion of innovations model (Rogers 1995), transtheoretical approach (Prochaska and DiClemente 1983) and social marketing approach (Kotler et al. 2002), but each of these occupies a small, specialized niche in the practical world of behaviour-change programmes.) Both types of approaches begin with the assumption that behaviour maximises expected utility. That is, behaviour is driven by the choice of that future outcome which is most highly valued, discounted by beliefs about how likely it is that such an outcome can be achieved. Similarly, self-help programmes typically rely on willpower, a high-level form of cognition which is known to be limited in important ways (Baumeister and Tierney 2012), while policymakers have normally assumed that people respond rationally to the constraints their policies place on people’s activity (Coleman 1990; Riker and Ordeshook 1973).

But campaigns that emphasize enhancing knowledge or altering attitudes frequently have little effect upon behaviour; there is often a weak relationship between attitudes and/or knowledge and behaviour (Armitage and Conner 2001; McKenzie-Mohr and Smith 2000). This is because the assumption of rational or cognitive causation is often false: Behaviour—or at least the behaviours of interest to behaviour-change specialists—is often largely caused by automatic (e.g. habitual) processes (Aunger 2007; Mittal 1988; Neal et al. 2012) and environmental factors (Stokols 1995), both of which tend to be ignored by expected utility models. For example, many illnesses are significantly influenced by the degree of economic inequality in a society (Wilkinson 2005), and physical activity depends upon civic resources for exercise (Owen et al. 2004; Sallis et al. 2006). Further, whenever behaviour-change models are augmented with demographic or environmental factors (Fishbein et al. 2001; Flay et al. 2009), these tend to be included as distal variables that have no direct impact on behaviour, but rather filter through cognition.

In contrast, an evolutionary approach begins with the assumption that behaviour has evolved to provide responses that were adaptive in the environment in which the animal in question evolved. In particular, the Evo–Eco approach sees behaviour as radically embodied and situated (Barker 1968; Barrett 2011; Clark 1997; Gibson 1979; Hutchins 1995). That is, factors other than cognition are considered active and present in the moment of behaviour, having independent causal influence on activity. For example, the environment is theorized to have its own structure and hence plays a formative role in behaviour production, rather than being seen as an amorphous set of 'barriers' (its typical role in behaviour-change models). Further, we emphasize the intrinsic dynamism of behaviour and its ephemeral nature, with the target behaviour occurring within a stream of prior- and post-activity. Thus, behaviour is seen as a dynamic interaction with other model elements, rather than as the consequence of previous steps in a linear causal model (the 'box-and-arrows' diagram other approaches tend to use).

Compared to health psychology and behavioural economics, then, our approach places greater emphasis on:

- The physicality of behaviour (physical environment, bodies)
- Place (e.g. space with designed infrastructure)
- Time (e.g. weekends)
- Brain-based mental processes (e.g. mental representation, goal achievement, memory)
- Objects and product design (especially synomorphic relationships)
- Different forms of learning (associative, affective and habitual as well as cognitive)
- Non-cognitive behavioural control processes (e.g. motivation, habit)
- Bodily states (e.g. hunger, sexual arousal)
- Behavioural dynamics (i.e. setting-based routines, chunking, sequence dependence)

Such a wide range of novel influences should provide rich new material and insights for effective behaviour-change programmes.

12.4 Using the Evo–Eco Approach

The Evo–Eco approach offers a new way of understanding the psychological and environmental determinants of behaviour. It organizes both well-established and novel factors derived from evolutionary biology of behaviour and ecological psychology into a simple schema of behaviour determination. But how does the approach help us to actually *change* behaviour?

It helps in a number of ways. First, the model can be used to generate hypotheses about the determinants of the behaviour that we seek to change. Second, we use it to organize field investigation of the target behaviours in formative research, testing whether our hypotheses about behaviour are correct and providing a structure for investigation. Third, we use the model to schematise the design principles for an intervention to change behaviour, and as a creative tool and, finally, we use it to explore the process by which behaviour change has come about, providing lessons for future efforts.

Below, we give a brief example of how the Evo–Eco model helped us design a successful intervention to change hand-washing behaviour in rural India. We describe how the model helped to organize formative research, helped to generate insights into the drivers of deeply habitual, ritualized and normative hygiene behaviour, helped us to come up with design principles for the campaign, how the intervention was tested and how we learnt something of the mechanisms of change that led to the intervention's success.

12.4.1 Hand-Washing Behaviour

Hand-washing with soap (HWWS) appears able to substantially reduce the risk of disease associated with infectious pathogens such as those that cause diarrhoeal disease and respiratory tract infections (Cairncross et al. 2010; Rabie and Curtis 2006). Though knowledge about the health relevance of HWWS is widespread, HWWS at key occasions is rare, for example, being practised by less than 20 % of people in low-income settings after the toilet (Curtis et al. 2011). New approaches are clearly needed that go beyond education to address the non-cognitive determinants of hand-washing behaviour.

12.4.2 Formative Research

Formative research is a phase of field-based investigation prior to intervention design which aims to provide design principles for behaviour change. In a series of formative research studies in 11 countries, we sought the factors that could be made relevant to changing hand-washing behaviour. While there was some variation from country to country, many of the drivers of hand-washing behaviour were common (Valerie Curtis et al. 2009). Pertinent aspects of the *physical environment* included lack of *infrastructure* (water was often scarce, although some was always available) and inappropriate or difficult-to-use *objects* such as basins placed on the ground, requiring stooping and soap bars that could not easily be used since they were slippery and fell on the ground. The *biological environment* played an important role in HWWS when there were epidemics such as cholera or bird flu; however, we found that HWWS tended to return to baseline once epidemics were perceived to be over (Fleischman et al. 2011). The *social environment* played an important role, with much hand-washing happening in public. In the UK, we found that HWWS increased when more people were present in a public toilet (Judah et al. 2009). However, in low-income settings, we found hand-washing not to be the norm, and the *settings* tended to correct behaviour away from HWWS, as mothers were sometimes accused of being profligate with water and soap and mocked by neighbours for being too fastidious. In behavioural trials, we saw how physically difficult it can be for *bodies* to actually manage the practice of HWWS, juggling infants, water jugs, soap and waste water with multiple other daily tasks.

As regards the *brain* aspects of the Evo–Eco model of hand-washing, we found that HWWS was a reflexive *habit* for some; however, these people tended to be exceptional, perhaps because of working in the health sector, having a particular upbringing or being excessively concerned about contamination. Hygiene rituals, however, were deeply habitual, with washing routines being highly stereotypic and almost identical from person to person across whole villages. *Motives* for hand-washing included *disgust,* the concern that contamination from toilets was brought into the home environment on hands, and making them smell bad; *nurture,* the desire to see a child responding to love and caring by being happy, thriving and successful; *affiliation,* which influenced mothers to wash their hands less (in tune with local norms, which did not involve practising HWWS) and *status,* in which hygienic people were, on the whole, admired and respected. The formative research used methods including filming, behavioural trials, motive mapping and settings observations and did not rely on verbal accounts by target groups and key informants to get insights into the drivers of hand-washing behaviour.

12.4.3 Design Principles

Design principles are the key determinants of behaviour which a campaign seeks to use as ‘levers of change’. Most public health behaviour-change campaigns in the developing world are based around approaches that target intentional change—that is, cognitive, often conscious decision-making on the part of the target population, as the most popular health psychological approaches deal exclusively in such variables (see section above). Figure 12.4 shows the design principles that we developed from the insights from formative research using the Evo–Eco approach. We asked a local Bangalore-based creative agency to focus on *disgust* and *nurture* and to try and change local norms, through making HWWS seem common and introducing hand-washing as good manners. We asked them to look at how to change *settings,* such that there were physical reminders to serve as cues, and for there to be social support for hand-washing from influential members of society. We also asked them to focus on inserting HWWS into daily routines. Changing the infrastructure and objects involved in hand-washing proved infeasible, as expected, in a rapid intervention, but is planned for other initiatives (working with the private sector to redesign soap and hand-wash stands). We briefed the agency not to rely on cognitive approaches, such as talking about diarrhoea and disease, although we did allow, on the basis of prior success, that mothers could be asked to express their intentions to HWWS in public pledges.

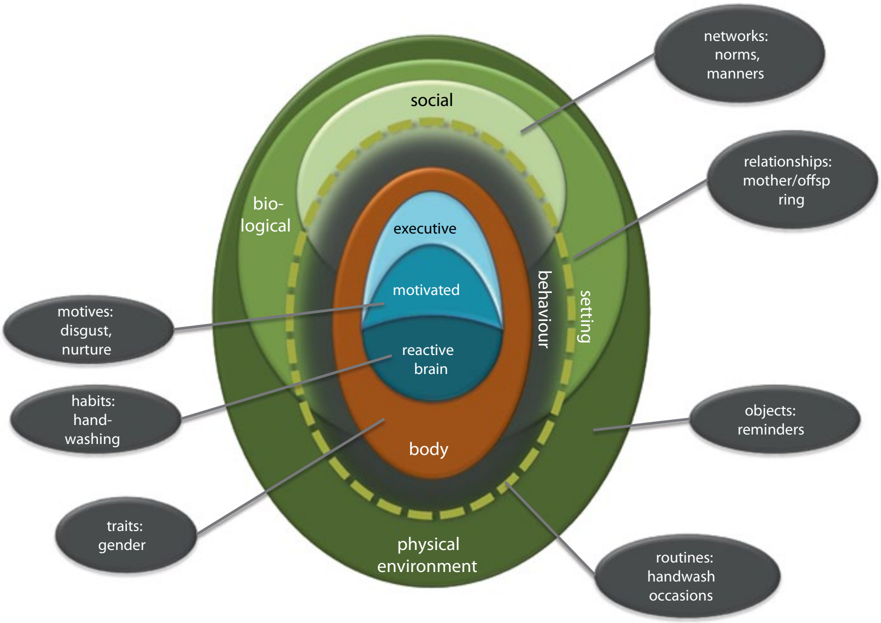


Fig. 12.4 Hand-washing trial design principles

A further part of the challenge to the creative agency was to design the HWWS intervention in such a way that it could be delivered by only two people over 2 days in each village. This was because we wanted an intervention that was capable of being scaled to the whole of India. The design team developed and tested a multi-faceted campaign that involved school children, community events, neighbourhood visits and a village rally. Activities included the showing of a cartoon film (http://www.youtube.com/watch?v=tLoNTe9ifCA) with a powerful emotional message about a mother (Super *Amma*) teaching child manners including hand-washing and being rewarded with its success and love.

12.4.4 Content of the Intervention

To change the social environment in favour of HWWS, we involved village authorities such as the *Sarpanch* (village chief), school and preschool teachers. Short video clips of them making statements about HWWS were shown at community events and their images appeared in HWWS posters that were displayed in public places. These individuals also appeared in person at the two community events. Women were asked to pledge to HWWS in public and when they did so, stickers were placed on their doors identifying them as HWWS supporters; their names also went up on a public display board in the centre of the village. Children also participated in a rally around each village to add to the 'presence' of HWWS as a norm.

12.4.5 Behavioural and Process Outcomes

The intervention was run in seven villages; HWWS behaviour was measured at start and finish and at several times following the intervention in intervention and control villages. The full details of this randomized controlled trial are described elsewhere (Biran et al. accepted). In brief, this experiment showed that directly observed HWWS went from being virtually absent (about 2 % in both intervention and control groups) to being practised by roughly one-third of the population, 6 months post intervention. Process indicators showed that there was also a significant shift in the proportion of people who reported thinking that HWWS was a social norm in their village (from 8 to 35 %).

12.5 Conclusion

Behaviour is an evolved phenomenon. Evolutionary theory is therefore the obvious place to start if one wishes to understand, and ultimately change, behaviour. While some approaches to behaviour change reflect some evolutionary reasoning, the Evo–Eco approach is the first comprehensive approach to behaviour change based explicitly on evolutionary theory. (Recently, there has been another call to base behaviour change in evolutionary theory (Wilson et al. in press). However, the strategy advocated in this case is restricted largely to intentional cultural evolution, or self-aware change by small groups or communities, which we believe is too restrictive, as it may be difficult to get explicit agreement from groups of the need for behaviour change, especially as many public health behaviours are practised habitually so that awareness of the need for change may be low.) The Evo–Eco approach is also current with relevant sciences, including content from neuroscience and psychology—sources broader than the cognitive psychology that constitutes the foundation of behaviour-change approaches in health psychology and behavioural economics.

The Evo–Eco model has the advantage of being more comprehensive than alternatives, including explicit treatment of the environment and body, not just the brain, and so provides a much richer source of potential insights. It emphasizes behaviour as a complex, dynamic interaction between bodies and environments. It focuses squarely on behaviour in settings and not on cognition and self-report as the locus for proper understanding (Barker 1968; Baumeister et al. 2007). With its view of the brain as an evolved organ, not a failed computer (as in behavioural economics), the Evo–Eco approach also provides a more positive view of human capabilities; rather than trying to make use of ‘biases’, it emphasizes the behaviour-change ‘problem’ as one of channelling natural, internally generated action impulses. People are naturally active—in order to stay alive in constantly changing environments, we must explore our surroundings to keep up to date on what threats and opportunities have arisen (Aunger and Curtis in press; Freeman 1999). The Evo–Eco approach can be seen as seeking to help people harness this ‘energy’ more profitably.

Of course, the ultimate proof of utility is evidence that the approach changes relevant behaviours. In this regard, the Evo–Eco approach has been used to develop a scalable programme to promote HWWS after key events in rural Indian villages. Based on this success (and earlier successes with precursors to this general model; Curtis et al. 2001; Scott et al. 2007), Evo–Eco is currently being used to develop interventions in other projects, such as child complementary feeding practices in Indonesia and multiple behaviours related to diarrhoea prevention in Zambia.

Another proof of the utility of any theory is its ability to help people generate novel predictions. One such prediction was that the ability to learn to repeatedly perform a novel behaviour within a behaviour setting is affected by its placement in the setting's routine. We have demonstrated that this routine placement effect is significant when learning a new flossing habit (Judah et al. 2012).

The Evo–Eco approach has thus been shown to change behaviour in public health projects and to inspire new empirical hypotheses about constraints on behaviour change in real-world contexts. We believe it has great potential to be used by public health workers and (social) marketers to devise more effective campaigns, by policymakers to improve general well-being and perhaps also by the general public as inspiration for their own self-help projects.

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