Synthesis in the Human Evolutionary Behavioural Sciences

Running title: the human evolutionary behavioural sciences

Rebecca Sear[1][2]
Department of Social Policy
London School of Economics

David W. Lawson
Human Evolutionary Ecology Group
Department of Anthropology
University College London

Thomas E. Dickins
School of Psychology
University of East London

&

Centre for Philosophy of Natural and Social Science
London School of Economics

[1] Corresponding author. Address: Department of Social Policy, London School of Economics, Houghton St, London WC2A 2AE, UK. Tel: 020 7955 7348. Fax: 020 7955 7415. Email: r.sear@lse.ac.uk
[2] All authors contributed equally to this paper. We have ordered authorship in reverse alphabetical order

Abstract

Over the last three decades, the application of evolutionary theory to the human sciences has shown remarkable growth. This growth has also been characterised by a 'splitting' process, with the emergence of distinct sub-disciplines, most notably: Human Behavioural Ecology (HBE), Evolutionary Psychology (EP) and studies of Cultural Evolution (CE). Multiple applications of evolutionary ideas to the human sciences are undoubtedly a good thing, demonstrating the usefulness of this approach to human affairs. Nevertheless, this fracture has been associated with considerable tension, a lack of integration, and sometimes outright conflict between researchers. In recent years however, there have been clear signs of hope that a synthesis of the human evolutionary behavioural sciences is underway. Here, we briefly review the history of the debate, both its theoretical and practical causes; then provide evidence that the field is currently becoming more integrated, as the traditional boundaries between sub-disciplines become blurred. This article constitutes the first paper under the new editorship of the Journal of Evolutionary Psychology, which aims to further this integration by explicitly providing a forum for integrated work.

Key Words: Human Behavioural Ecology, Evolutionary Psychology, Cultural Evolution

1. Introduction

The application of Darwinian thought to the human behavioural sciences, beginning in earnest with the publication of Wilson's *Sociobiology: The New Synthesis* in 1975, has had a turbulent history. Sociobiology applies gene-level selectionist models directly to behaviour enabling both the explanation of the ultimate causes of behaviour, and the prediction of specific behaviours under a variety of ecological conditions. The rather hostile reception of these ideas by the social sciences is well documented (see Segerstråle 2000 for a excellent account). Our concern here is not with the misinterpretation of evolutionary theory by the social sciences, but the 'splitting' process that the human evolutionary behavioural sciences have undergone over the last three decades. Broadly speaking, three sub-disciplines have emerged: Human Behavioural Ecology (HBE), Evolutionary Psychology (EP) and studies of Cultural Evolution (CE). This internal fracture has been tracked by a consistent flow of papers and books (Crawford 1993; Sherman and Reeve 1997; Daly and Wilson 1999; Heyes 2000; Smith 2000; Smith *et al.* 2000; Downes 2001; Smith *et al.* 2001; Barrett *et al.* 2002; Laland and Brown 2002; Hutchinson and Gigerenzer 2005; Kaplan and Gangestad 2005; Dunbar and Barrett 2007b; Gangestad and Simpson 2007a; White *et al.* 2007). See Table 1 for a list of articles which have reviewed or attempted to synthesise these sub-disciplines, many of which provide informative summaries of the key issues.

INSERT TABLE 1 ABOUT HERE

Here we provide our own overview of the key boundaries that have arisen, but emphasise that in recent years there is strong evidence that a reintegration of the discipline is on the horizon. We argue that theoretical synthesis, while still far from ubiquitous, has become a significant feature of the contemporary literature. Traditional methodological

boundaries have also attenuated, and some genuinely integrated research programmes and research groups have arisen in recent years. We briefly consider the role of relevant studies beyond our three-way split, and the rise of applied, rather than purely academic, studies, before concluding with some optimism that a synthesis of the human evolutionary behavioural sciences is truly underway. We start with a brief description of each of the three sub-disciplines.

2. The Three Approaches

2.1 Human Behavioural Ecology

HBE emerged directly from Sociobiology (Wilson 1975), inheriting a core concern with the ultimate functions of behaviour rather than its underlying mechanisms. Throughout this article, we concentrate on HBE as a subcategory of human evolutionary ecology (an umbrella term including applications to non-behavioural aspects of the phenotype), as the focus of this paper is the behavioural sciences. However, we note that most of the points could be applied to human evolutionary ecology at large.

HBE is concerned with explaining adaptive behavioural variation within its ecological context. Organisms are understood to be attempting to maximize their fitness under specific ecological conditions. Today, HBE remains virtually identical in approach to animal behavioural ecology (e.g. Krebs and Davies 1993), using the same tools and techniques, such as optimality theory (Parker and Maynard Smith 1990), to generate testable predictions (Borgerhoff Mulder 1991; Cronk 1991; Winterhalder and Smith 2000). At the heart of HBE lies a black box approach to understanding the traits in question, referred to as the phenotypic gambit (a term first coined by Grafen, 1984). This assumes that there is some linkage between genes and behaviour, and therefore behaviour can be analysed in ultimate terms, but the nature of this linkage is not an explicit concern. HBE explains behavioural variation using

the concept of phenotypic plasticity, which assumes that the same genotype can give rise to multiple phenotypes dependent on ecological conditions. Testing models requires that the fitness differentials associated with behavioural strategies are identified. As long-term fitness is difficult to measure directly, proximate outcomes are used as proxy measures, most commonly number of children or grandchildren, but also alternative measures such as health or social status outcomes. Such models have performed well, and demonstrated predictive power in a variety of domains, such as foraging, mating and parental investment (Winterhalder and Smith 2000 for a review).

2.2 Evolutionary Psychology

In contrast to the phenotypic gambit approach of HBE, the focus of EP is upon the proximate psychological mechanisms that cause behaviour. The broad conception of EP is that proximate psychological mechanisms will be better understood in terms of their ultimate functions. Put more prosaically, given that the brain is an evolved organ, there must be some interesting theoretical constraints upon psychological theory from evolutionary biology. Under this formulation there is a lot of room for different approaches to the application of evolutionary biology to psychology, some of which would not necessarily be that removed from HBE. This broad conception of EP is to be regarded as theoretically integrative. However, one particular school of thought has dominated EP, which emerged primarily (but not exclusively) from the University of California, Santa Barbara (Barkow *et al.* 1992). This school has actively sought to differentiate itself from HBE, principally on theoretical grounds. This distinction has been noted by a number of authors (e.g. Downes 2001; Gray *et al.* 2003; Buller 2005; Dunbar and Barrett 2007a), though it is not universally accepted within EP. Nonetheless, we find the distinction useful and will adopt Dunbar and Barrett's (2007a) terminology of EP *sensu stricto* (EPSS).

Unlike the broad conception of EP, EPSS has some firm views on the precise nature of psychological adaptations. EPSS characterises these adaptations as domain-specific, claiming that this is a consequence of evolution by natural selection, for natural selection only selects adaptations that solve specific problems (though see Atkinson and Wheeler, 2004, for a discussion of degrees of domain specificity). Given this, each psychological adaptation was selected to solve a particular ancestral problem, and as such each adaptation has its own Environment of Evolutionary Adaptedness (EEA; *pace* Bowlby 1969) which is the specific environment in which the adaptive problem presented itself and was solved. In the canonical book, *The Adapted Mind* (Barkow *et al.* 1992) this Pleistocene EEA epoch was described as a period of sustained and consistent selection pressures. EPSS has now hypothesised specific mechanisms relating to such diverse factors as – fear of snakes, detection of social cheats, language acquisition, preference for foods rich in fats and sugar, sex differences in sexual jealousy and mate preferences (relating to economic resources, age, attractiveness, body shape and sexual variety), and even landscape preferences for savannah like environments (reviewed in Buss 1995). These mechanisms are seen as universal species-typical adaptations with any cultural and individual differences explained by their regulated interaction with local environmental conditions (Tooby and Cosmides 1992).

Domain-specificity was subsequently discussed in terms of cognitive modularity (Fodor 200; Atkinson and Wheeler 2004). The architectural descriptions given in *The Adapted Mind* conform to aspects of modularity theory in that they assume specific content and specific processing for each adapted mechanism. This has led some to refer to this position as Darwinian Modularity, in contrast with Fodorian Modularity, which is process based, and Chomskyan Modularity, which is content based (Samuels 1998; Samuels 2000). The position EPSS takes on modularity is a consequence of theoretical commitments within

cognitive science (Dickins 2003). The idea that psychological adaptations are domain-specific and modular is core to EPSS.

2.3 Cultural Evolution

CE shares some important commonalities with both HBE and EP (Henrich and McElreath 2003). Like HBE, CE is often concerned with the current adaptive utility of traits (although it has also considered the emergence of maladaptive behaviours: e.g. Boyd and Richerson 2005). Like EP, it is also interested in the proximate mechanisms by which behaviour is brought about, albeit specifically with mechanisms of social learning and transmission of cultural traits rather than underlying cognitive apparatus. However, it differs from both in its conviction that a robust understanding of human behaviour requires explicit consideration of cultural as well as genetic evolution. This focus on the cultural transmission of behavioural traits, studied at the within and between population level, sets CE apart from the largely individual level work of the other two sub- disciplines.

We should note at this point that our tripartite split glosses over some distinct traditions within CE, and that the field itself is not particularly unified. Many researchers stress a distinction between memetics and gene-culture coevolution (Laland and Brown 2002). Broadly speaking, memetics considers cultural evolution to be entirely divorced from biological evolution, though the evolution of cultural practices can be modelled along similar lines to those of genetic evolution (Aunger 2000). This branch of enquiry is a considerably smaller area, and has come under harsh criticism for a number of controversial assumptions, and a reliance on purely theoretical application (see Laland and Brown 2002). We focus more specifically on gene-culture coevolution (also known as dual inheritance theory), a larger and rapidly growing area that considers human genetic and cultural inheritance to be decidedly interdependent. A mathematical focus unites much of this research and the techniques of

population genetics are commonly used to model the dynamics of cultural transmission and the interaction of biological and cultural evolutionary processes (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Feldman and Laland 1996; Henrich and McElreath 2003; Richerson and Boyd 2005).

We now lay out in turn the theoretical, methodological and sociological issues which have distanced the three sub-disciplines, but in each section provide evidence that resolution may be underway in each area.

3. Theory

HBE and EPSS have historically been at odds with one another (see, for example Symons 1989; 1992; Daly and Wilson 1999; Smith *et al.* 2000), and CE has been somewhat marginalised. Below we briefly describe the theoretical arguments between HBE and EPSS. We then go on to explain why we take the view that, on the whole, there are no insurmountable theoretical boundaries between EPSS and HBE. Finally, we discuss the extent to which CE can also be integrated into a wider framework.

3.1 The HBE/EPSS Dispute

The core difference between HBE and EPSS has been captured by the distinction between fitness maximizers and adaptation executors (Tooby and Cosmides 1992). HBE (the former) assumes that behaviours are adapted to current ecologies, and EPSS (the latter) assumes current behaviours are the products of ancestrally selected psychological adaptations. EPSS has used this distinction to criticise HBE for being naively adaptationist, and providing no explicit method for distinguishing an adaptation (Symons 1989; 1992). The HBE research programme assumes extreme phenotypic plasticity which EPSS characterises

as an emphasis on humans as unconstrained fitness maximizers and argues that this implicitly advocates a domain-general cognitive system (Buss 1995). This directly contradicts EPSS's defining assumption of domain-specificity. In turn, the claim of EPSS that psychological mechanisms are adaptations to past environments has led to HBE criticism that EPSS puts a misleading over-reliance on a simplistic hypothesis of our ancestral environment (Foley 1995; Irons 1998; Potts 1998; Strassmann and Dunbar 1999). Furthermore, it is claimed that a consequence of this focus is that EPSS emphasises human universals at the expense of exploring the full behavioural repertoire of our species (Gray *et al.* 2003).

3.2 Resolutions

The theoretical disagreements between HBE and EPSS have involved a considerable amount of misinterpretation. It is not unusual to draw lines in the sand using extreme descriptions of alternative positions, especially in the early days of a discipline, but this hinders integration. These disagreements have centred on the following three issues: the role of adaptive fit to current environments; with the domain-specificity or otherwise of the proximate psychological mechanisms; and, with the role of human universals versus variability.

The domain-specificity problem is easy to dismiss, as EPSS and HBE do not need to disagree on this issue at all. HBE is agnostic about the proximate mechanisms by which traits are brought about, and therefore has nothing to say about whether psychological mechanisms are domain-specific or not (Smith *et al.* 2000). Thus, the phenotypic gambit neither commits HBE to a domain-specific nor to a domain-general cognitive architecture: its focus is exclusively upon the behavioural outcome. As to specific notions of modularity, this debate should be used to forward the field by generating research which aims to test hypotheses about the specific nature of psychological mechanisms (see Brown 2001; De Winter and Oxnard 2001; Menzel and Giurfa 2001 for examples from the non-human

literature). Quarrels about the nature of cognitive architecture should certainly not be allowed hold up the integration of the field, since this is a question open to empirical testing.

Turning to the issue of universals versus variability, this is also perhaps not quite as divisive as it might appear. EPSS, for example, is quite explicit that observed behaviour results from the interaction of a universal human nature with environmental conditions, such that behaviours are contingent, just as HBE assumes. Psychological mechanisms themselves are to be seen as conditional, or decision architectures, just as genes and other biological systems are (Dickins and Dickins 2007). This can work in two ways: (1) we have an evolved capacity to remember stimuli and make associations between them, for example, but the actual remembered material and associations made are a consequence of external factors and their salience in a given ecology; and, (2) psychological mechanisms are information processors designed to make judgements about best utility, which means that they embody strategies for different contingencies. This latter notion is incorporated in psychological work on future discounting (Daly and Wilson 2005) as well as work on more deliberative judgement and decision-making (Gigerenzer and Todd 1991). It would be a peculiar notion of a psychological universal if it only allowed for one possible behavioural output. The disquiet about claims to psychological universals, which arises from observations of behavioural variation, amounts to no more than a grain-problem. The level granularity required to claim behavioural variation is different from that used to claim psychological variation. Psychological mechanisms are discussed in terms of the type of thing they do, and behaviour (at least for HBE) is often focused on at the token level: so, there are mechanisms for memory (for example, procedural memory for doing and making things) and there are the actual memories that different groups value (for example, how to make a canoe versus how to make a dinghy). Thus, EPSS can safely lay claim to the human universal of procedural

memory, whilst HBE is right to focus on variability in the actual products. Such a distinction can be made across all of human activity.

Finally, we need to deal with the issue of adaptation to past versus current environments. This is also not necessarily polarising, but it has produced the most heated arguments between HBE and EPSS. Clearly, many of the problems faced by our species, to which we might have evolved adaptations, have been around for a very long time, and the potential solutions are likely to have evolved sometime during our past. Additionally, there are some aspects of the modern industrialised world which are novel, and it is possible we may be responding non-adaptively to them. Equally clearly, there is strong evidence that adaptations have continued to form in response to selection during the Holocene epoch (*e.g.* Hill *et al.* 1991; Holden and Mace 1997; Williamson *et al.* 2007), including evidence for the evolution of genes mediating neural design (Evans *et al.* 2005; Mekel-Bobrov *et al.* 2005). It is also likely that even Pleistocene hunter-gatherer environments were considerably diverse, rather than presenting a set of static homogenised selective pressures, given the wide geographical range hominins and early humans colonised (e.g. Dennell and Roebroeks 2005). HBE of course does not deny that there were crucial selective environments in the past that shaped the underlying proximate mechanisms that in fact deliver behaviour; it is just that the phenotypic gambit renders theories of these environments inconsequential. Nor do they naively assume that every trait is optimally adapted to its current environment (there is an implicit recognition of this in the fact that HBE has largely restricted its analyses to traditional societies). On the other hand, EP rarely operates according to a stringent Pleistocene notion of the EEA (Daly and Wilson 1999), though some researchers within EPSS do (e.g. Symons 1992; Kanazawa 2004). Most EP researchers look at modern behaviours and try to hypothesise the adaptive utility of the current behaviour. This is clearly evident, for example, in the mate-preference literature, which assumes that modern mating

decisions are governed by universal dispositions that are effectively designed to maximize fitness (though exactly how such dispositions present themselves may vary according to environmental conditions). The main points of attraction, such as symmetry, are argued to be indicative of developmental stability which is a current concern, as well as presumably one for our Pleistocene ancestors and beyond. It is only when non-adaptive behaviours present, that hypotheses about ancestral environments aid the development of mismatch explanations. Some evolutionary psychologists are also coming round to the idea that there may well be genetic differences between populations that affect behaviour, as has been shown for a number of physiological traits (Nettle 2007). This of course means there has been a diversity of selection environments.

So we believe the theoretical differences between HBE and EPSS to have been somewhat over-emphasised in earlier writings. However, we do not mean to suggest that all theoretical differences are now resolved. Debates still remain, for example, on the extent to which particular behaviours are universal versus ecologically variable, or the extent to which behaviours are adapted to current environments. But these debates are now being subjected to empirical testing (see, for example, Section 4.2 on the rise of cross-cultural work), rather than used as evidence of irreconcilable theoretical differences that hold up the synthesis of the discipline.

3.3 The Cultural Evolution Position

Despite CE's relatively long history (Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981) it has largely been ignored by the EP and HBE literature (for example, in the 2-year period before 2007 only 8% of articles in the main journal in the field, *Evolution & Human Behavior*, considered culture as the topic point of interest: Hill 2007). The focus of EPSS on human universals means it has paid relatively little attention to cultural differences,

and where it does allow for cultural differences there is a tendency to assume they are 'evoked' (i.e. the result of context-dependent psychological mechanisms interacting with local environments) rather than 'transmitted' (i.e. the result of social learning: Tooby and Cosmides 1992; Gangestad *et al.* 2006; Mameli 2007). HBE has tended to brush aside the issue of culture by assuming that cultural differences between populations are simply part of the environment, rather than make cultural variation itself the focus of their investigations. As part of the phenotypic gambit it does not directly concern itself on the matter of whether behaviour is brought about through purely genetic evolution, cultural evolution or gene-culture evolution, only the extent to which the end result fits adaptive predictions.

Its interest in current adaptiveness means that theoretically CE is more closely aligned with HBE than EPSS. Much of the previous discussion on the differences between HBE and EPSS therefore also applies to differences between CE and EPSS. Given that CE is not yet a particularly unified field, and that it is at an earlier stage of development than either HBE or EPSS, theoretical debates in CE often revolve around disputes within the field itself: for example, the extent to which cultural evolution is inter-related with genetic evolution (Laland and Brown 2002); and debates around the importance of horizontal versus vertical transmission of cultural traits between populations (Mace and Holden 2005; Borgerhoff Mulder *et al.* 2006; Collard *et al.* 2006). Part of the reason for the marginalisation of CE does, however, hinge on theoretical differences of opinion on the importance of culture in explaining human behaviour. Some within EP and HBE take the reductionist view that cultural practices simply result from individual behaviour, and therefore that the action of natural selection will select for behaviours that operate in a group context. A separate study of cultural behaviour is therefore not really necessary: adaptations or adaptive behavioural variability can be predicted without recourse to culture (Alvard 2003; Dickins 2005). There is also some unease about the introduction of cultural evolution into the evolutionary

behavioural sciences from at least some members of both the HBE and EP camps. Genetic evolution through natural selection is a long-established and (reasonably) well understood phenomenon, even if its application to human behaviour is relatively new. The evolution of cultural traits through mechanisms analogous to genetic evolution (though integrated with genetic evolution) appears to some to be, firstly, stretching the analogy of Darwinian evolution too far; and secondly, uncomfortably close to the post-modern approach to human behaviour, with its associated lack of scientific rigour (Alvard 2003).

But overall, theoretical disagreements between CE and the other evolutionary behavioural sciences (over and above those between HBE and EPSS) are relatively minor: both HBE and EP largely admit that (transmitted) culture exists and matters at least to some extent to human behavioural evolution, even if the extent to which it matters, and the degree to which researchers think it necessary to include culture explicitly in their models, varies considerably. The marginalisation of CE by the other sub-disciplines may, in practice, have more to do with methodological differences, to which we turn in Section 4. In summary, CE does not appear to have the programmatic aims of HBE, EP and especially EPSS. CE researchers are individually engaged in specific investigations that would be happily incorporated within the broader human evolutionary behavioural sciences. CE represents no threat to integration, but a fertile ground for cooperation. For example, Laland and Brown (2006) have suggested that the ability of our species to construct our own niches allows us to buffer ourselves against adaptive lag, so that behaviour even in modern industrial environments may well be adaptive. This is relevant to HBE/EP debates surrounding the EEA and notions of environmental mismatch.

4. Methodology

4.1.1 Methodological Differences

We now turn to more pragmatic reasons for the 'splitting' of the human evolutionary behavioural sciences. Substantial methodological differences have exacerbated theoretical divisions. Differences in preferred study populations, and methods of data collection and analysis have hampered communication and potential pathways to synthesis. In terms of study population, HBE has so far almost exclusively focused on traditional populations, with high fertility and mortality rates (and therefore high variance in the traits HBE is most interested in). In contrast, the vast majority of EPSS studies have been conducted on modern industrialised populations. There is an inherent irony in this division: EPSS lays much emphasis on identifying universal preferences, yet focuses almost entirely on Westernised populations, while HBE has assumed that its methods should be successful in any type of environment, yet have largely ignored the region in which most of them reside. For example, although cross-cultural analysis was not entirely lacking from early EPSS work, it tended to be relatively unconvincing at least to the anthropologically-trained HBE community. Buss' (1989) highly cited work claiming to find consistent sex differences in mate preferences across 37 cultures used no fewer than 24 samples from groups which were European or derived from European populations (e.g. US, Australia, South African whites). And those non-Western populations which were included tended to be rather more 'Westernised' than the small-scale traditional populations HBE has been interested in. On the other hand, EPSS researchers may well consider HBE's decision to ignore their preferred study population as an implicit recognition that their models hold little explanatory power when applied to the modern industrialised world. Therefore, these differences have traditionally left researchers on either side of the debate unconvinced by the potential relevance of the sister research programme.

Differences in methods of data collection and analysis are also apparent across the sub-disciplines. HBE researchers approach human behaviour from a background in animal behavioural ecology or anthropology, both of which have long running traditions of fieldwork, collecting data from observed behavioural outcomes. EPSS researchers, in contrast, trained in psychological methods that use self-reported preferences or experimental manipulations of behaviour, maintain that this is sufficient for distinguishing between alternative hypotheses about human psychology. For HBE, observational methods enable perfect ecological validity; an assessment of variable phenotypic expression in its true selective environment. For EPSS, experimental methods offer high reliability in controlling for independent variables that may otherwise confound results.

CE once again is best considered separately, since, initially at least, its methods focused almost exclusively on theoretical modelling rather than empirical study. While this approach is undoubtedly important in the evolutionary tool-kit, it has its drawbacks. Of necessity, strict assumptions need to be applied for reasonably simple models to be produced, which make it difficult for empiricists to relate such models to real world situations. Secondly, few researchers trained in empirical methods are also trained in mathematical modelling. While mathematical modelling is not entirely alien to other behavioural scientists, in order to clarify relationships in observed data, it is usually a minor component of their approach. An over reliance on purely theoretical modelling by CE may distance it from empirical scientists. In addition, though it purports to be interested in the mechanisms of social transmission between individuals, CE research on exactly how individuals do transmit information to each other was traditionally lacking. Various mechanisms have been proposed to explain which individuals people choose to obtain social information from (for example, conformist bias – behave like the majority; prestige bias – behave like the most successful members of the community) but the theoretical modelling of such transmission biases is

rather more advanced than the study of how such social transmission works on the ground (e.g. Boyd and Richerson 1985; Henrich and Boyd 1998; Eriksson *et al.* this volume). This methodological division between theoretical and empirical approaches is perhaps one of the principal reasons why CE has been somewhat sidelined in the human evolutionary behavioural sciences.

4.2 Narrowing the methodological divide

Movements to theoretical integration have been echoed by a softening of historical boundaries in methodology. It is encouraging that, while HBE research is still biased towards traditional populations, its theoretical framework is increasingly being applied to modern industrialised societies. One particular area of focus has been reproductive decision making. In part, this has been a direct response to early claims (e.g. Vining 1986) that adaptive models of human behaviour are clearly falsified by the emergence of negative or null relationships between wealth and fertility that characterise modernisation (Borgerhoff Mulder 1998). A significant body of research has now emerged encompassing both theoretical and mathematical modelling of the relationship between wealth and family size across multiple generations (Mace 1998; Hill and Reeve 2005; McNamara and Houston 2006) along with directed empirical study (most notably Kaplan *et al.* 1995a; Kaplan *et al.* 1995b). Apparent mismatch between Western family size and the seemingly low ecological costs of child-rearing has led HBE to incorporate models from EP and CE. For example, the work of Kaplan and colleagues (1995a; 1995b; 2002) has a distinct integrative flavour, containing hypotheses about underlying psychological adaptations of fertility regulation that have predictive utility. While reviews of the evolutionary approach to demographic transition by prominent HBE researchers (Borgerhoff Mulder 1998; Mace 2007) have included integrative discussions of relevant studies in EP (e.g. Perrusse 1993) and CE (e.g. Newson *et al.* 2007).

Clearly this is a potential further stimulus to theoretical development and synthesis in its own right.

Perhaps the methodological development most likely to promote integration is the increasing inclusion of relatively non-Westernised societies in EP research. An active movement to test models amongst a more representative set of human cultures is clearly underway. Many EP researchers are now testing models in non-Western populations (e.g. Barrett and Behne 2005; Brown *et al.* 2005; Hagen and Barrett 2007), and others are attempting to reassess earlier demonstrations of universality with more diverse datasets (e.g. Moore and Cassidy 2007). Although including understudied traditional populations, such as hunter-gatherer groups, may be difficult in such large scale analyses, the potential contributions are illuminating. For example, Moore and Cassidy (2007) have made efforts to include societies with relatively high degrees of female access to resources in a cross-cultural study of mating preferences. The study suggests that EPSS claims for universal sex differences in the prioritisation of wealth in potential mates requires reconsideration. Similarly, recent work by authors such as Furnham and Swami suggests that male preferences for female phenotypic characteristics may be more diverse than implied in some EPSS research (Furnham *et al.* 2002; Swami *et al.* 2006; Tovee *et al.* 2006; Swami and Tovee 2007). In general it appears that a fuller discussion of the role of contingency in psychological mechanism and of cross-cultural differences in EP literature is emerging, thereby increasing its relevance to HBE and CE. This development can only improve relations between the sub-disciplines.

There are also notable developments in the CE literature as its researchers are increasingly applying models to real data, at both the macro- and micro-evolutionary level. At the macro level, researchers are beginning to use comparative methods to test adaptive hypotheses about cross-cultural variation in cultural traits (McElreath 2004; Henrich *et al.*

2005). In particular, the emerging field of cultural phylogenetics has had success in explaining variation in traits such as lactose tolerance, sexual dimorphism in height and marriage practices (Holden and Mace 1997; 1999; Mace and Holden 1999; Borgerhoff Mulder *et al.* 2001; Fortunato *et al.* 2006). At the micro level, CE is slowly moving into the lab using both Western and non Western participants. Studies of social transmission in action are beginning to appear in the literature (Baum *et al.* 2004; McElreath *et al.* 2005; Mesoudi *et al.* 2006; Efferson *et al.* 2007), and a recent call has gone out to CE practitioners to incorporate the methods of social psychology into the discipline to gain a better understanding of cultural microevolution (Mesoudi 2007).

The best demonstration of synthesis is collaborative research that genuinely integrates the methods of each sub-discipline. A particularly fruitful line of enquiry is cross-cultural research and there has been a recent surge of such projects. Such work can get to the heart of remaining debates about the level at which traits may be universal or variable between populations. A number of research projects have now been initiated with the aim of drawing together teams of researchers who pool expertise and study populations, in order to generate new databases of comparative data. Henrich and colleagues (2005), for example, combined laboratory EP with HBE field methods: participants from a range of small-scale traditional societies were given economic games to play, in order to explore and explain cross-cultural variation in self-interest. A similar collaboration currently in progress is the Demography, Ecology and Mate Choice project[3], run by Penton-Voak and Josephson and funded by the Leverhulme Trust. Other projects, bringing together existing databases and researchers across sub-disciplines, include the intergenerational transmission of wealth in pre-modern societies project at the Santa Fe Institute, organised by Bowles and Borgerhoff Mulder[4].

[3] http://www.demc.org
[4] http://www.santafe.edu/events/workshops/index.php/Overview:_Inter-generational_Transmission_of_Wealth_in_Pre-modern_Societies.

Individual research articles are also beginning to use mixed methods, combining more than one approach to the study of a particular question. For example, Newson et al. 2007 combines lab testing of participants with cultural evolution models to examine how conversations with kin vs. non kin may influence reproductive decision making.
And both Jones et al (2007) and Waynforth (2007) have recently combined the traditional preoccupations of CE and EP by looking at the social transmission of mate preferences.

Such collaborative ventures and the use of mixed methods raise the exciting prospect of gaining a much more detailed and complete understanding of human behaviour, by pooling the expertise of numerous scholars from diverse fields of enquiry but all working within an evolutionary framework.

5. Sociology

5.1 Issues

Just as it is important to identify methodological differences as a practical element in the 'splitting' of the discipline, we must also remember that theoretical debates do not occur in a sociological vacuum. Wilson's Sociobiology (1975) generated considerable controversy with neighbouring disciplines, not just the social sciences, but also biologists, many of whom were opposed to the application of evolutionary models to our own species' behaviour (e.g. Gould and Lewontin 1979; Lewontin *et al.* 1984; Rose *et al.* 2000). Internal debates within the human evolutionary behavioural sciences have always existed within a larger context of academic hostility. One might speculate that aggressive debates with neighbouring disciplines have exacerbated internal tensions, instilling a combative attitude to discussion.

Strains placed on the discipline by external hostility are magnified by departmental separations between sub-disciplines. EP is typically hosted within psychology departments, and HBE and CE within anthropology departments. The latter placements are somewhat

ironic, as neither HBE nor CE has taken significant theoretical inspiration from traditional anthropological studies. However, this has resulted in closer collaboration between HBE and CE than between EP and either of these areas. Several prominent HBE researchers have, perhaps as a consequence, moved into CE research areas (for example: Cronk 1999; Mace and Holden 2005; Borgerhoff Mulder *et al.* 2006). Physical separation of researchers hampers communication, and this enforced division pushes the discipline further apart in other ways, resulting in researchers publishing in different journals and attending different conferences. It could be that this is driven by an understandable desire to persuade other fields of enquiry of the usefulness of evolutionary theory, but it also occurs for more pragmatic reasons. For career advancement, evolutionary psychologists and anthropologists are required to build a reputation in their home disciplines. This means that it is their direct peers who will be reviewing their grants, applications for tenure and promotion. Necessarily this focuses activities within the relevant sub-discipline at the expense of engaging with other evolutionary sub-disciplines.

Distinct sub-disciplinary jargon is another barrier to integration which results from the different disciplinary backgrounds. For example, what HBE refers to as phenotypic plasticity, EPSS would term evoked culture. Phenotypic plasticity is an important component of behavioural ecology, and there has been much recent work on the topic in the biological literature (e.g. West-Eberhard 2003). However, 'plasticity' is not a word that seems to find favour with EPSS where it is seen as too vague a term to be useful (Hagen 2005). Phenotypic plasticity is not simply a vague statement that phenotypes can vary, however, but a rigorous concept: reaction norms can be predicted which stipulate exactly how a phenotype changes in response to environmental cues thereby demonstrating the conditional nature of phenotypic expression (e.g. Allal *et al.* 2004). HBE has in turn found fault with the EPSS phrase 'evoked culture', arguing that culture should be used only to describe socially transmitted information,

since there is much ‘evoked culture’ (i.e. adaptive behavioural variation in response to environmental conditions) in non-humans animals that is not usefully described as ‘culture’ (Alvard 2003). The term is not therefore useful, and may be unnecessarily confusing, when applied to our own species. The issues of terminology require resolution for if the sub-disciplines do not understand one another’s language, misunderstandings can easily arise.

Finally, the new and controversial nature of the discipline has enforced a strong concern for reputation. Researchers in the HBE and CE community have been particularly vocal about these concerns (Smith *et al.* 2001; Laland and Brown 2002). One major issue revolves around the relative dominance of EPSS in the popular media (Cassidy 2005; Cassidy 2006), with its attendant simplifications and lack of peer-review (Downes 2001; Gray *et al.* 2003). This media interest may be partly due to the focus of EPSS on Westernised society and on the perennially popular topics of attractiveness and sexual strategies. Whatever the case, the unfortunate consequence of this current dynamic is that assumptions about the evolutionary approach to human behaviour are more frequently based on knowledge of EPSS rather than any alternative approach. This often leads to a one-sided, and inaccurate view, of the human evolutionary behavioural sciences both by the public and other academic disciplines.

5.2.1 Solutions

Wider sociological issues may remain troublesome for the integration of the discipline until universities form unified departments of human evolutionary behavioural science. There are, however, already encouraging signs that some institutions are recognising that old disciplinary boundaries are out-dated, and combining evolutionarily-related departments and research groups in order to build more integrated units. Below we note a number of departments and research groups within the UK that contain representatives from more than one sub-discipline, rather than sequestering each into its home department. We restrict this

section to the UK, as it is the area with which we are most familiar, but we hope that similar integration is occurring in other regions of the world:

- the Centre for Evolution and Behaviour within the School of Biology & Psychology at the University of Newcastle
- the Evolutionary Psychology and Behavioural Ecology Research Group within the School of Biological Sciences at the University of Liverpool
- the Centre for Culture and Evolutionary Psychology within the School of Social Sciences at Brunel University
- University College London houses two research groups with much cross-fertilisation, whose members are drawn largely from the Department of Anthropology and the Institute of Archaeology, the Centre for the Evolution of Cultural Diversity and the Human Evolutionary Ecology Group

Even where institutions are not sufficiently enlightened to provide integrated departments, it is still possible to create 'virtual' communities of like-minded researchers. For example, the Work in Progress group at the London School of Economics was the crucible for this particular collaboration between EP and HBE.

We have recently developed another forum which explicitly aims to promote an integrative framework for future study: The European Human Behaviour and Evolution Conferences[5]. Initiated in 2006, the EHBE conferences bring together researchers from all branches of the human evolutionary behavioural sciences and are deliberately designed to encourage communication and dialogue between sub-disciplines. Sessions are serial allowing delegates to attend all sessions and strenuous attempts are made to ensure a balanced programme, with representation from all main branches of the field. For example, the 2007

[5] www.ehbes.com

conference devoted a day each to human behavioural ecology, evolutionary psychology and cultural evolution (though other branches, including evolutionary sociology, medicine and archaeology, were also represented, see Section 6). Papers presented at the 2007 conference have formed this opening issue under the new editorial board of the *Journal of Evolutionary Psychology*, which aims to become a similarly inclusive medium, interpreting psychology in its broadest sense to include HBE and CE.

6. Beyond HBE, EP and CE

Though we have divided the field into three for the purposes of this paper, not all researchers in the human evolutionary behavioural sciences align themselves with these camps. As the number of researchers on the field grows, new sub-disciplines are beginning to spring up and other social scientists are becoming interested in applying evolutionary ideas to their own discipline. Prominent examples of new sub-disciplines include:

- Reproductive ecology is an expanding branch concerned with understanding human reproductive physiology in adaptive framework (see Ellison 2001 or 2003)
- Evolutionary medicine (see Nesse and Williams 1995 for the seminal work in this field)[6].
- Evolutionary archaeology (O'Brien and Lyman 2002; Bird and O'Connell 2006).

Prominent examples of the application of evolutionary theory to the social sciences outside of anthropology and psychology include:

- Economics: activities in this area include the Economic and Social Research Council-funded Centre for Economic Learning and Social Evolution at University College London, established by Binmore. Publications in this field include: Frank *et al.* 1993; Gintis 2000; Bowles and Gintis 2002; Binmore 2005; Gintis *et al.* 2006

[6]see the Evolution and Medicine Network for more recent developments, http://www.evolutionandmedicine.org/.

- Sociology: activities include an Evolution and Sociology session at the European Sociological Association's 2007 conference. Publications include: Freese *et al.* 2003; Davis and Were 2007
- Demography: activities include the Evolutionary Biodemography working group at the Max Planck Institute for Demographic Research, Rostock; evolutionary demography sessions are now held at the annual conferences of the British Society for Population Studies, the Population Association of America, the European Association for Population Studies and the International Union for the Scientific Study of Population. Publications include: Murphy 1999; Lee 2003; Baudisch and Vaupel 2005; Hobcraft 2006

Mainstream biologists may also be coming round to the idea that human behaviour can be studied using the standard evolutionary principles applied to the study of non-human animal behaviour, as evidenced by the joint School of Biology and Psychology at Newcastle University; Lummaa's Human Life History Project in the Department of Animal and Plant Sciences at Sheffield University; and the UK Association for the Study of Animal Behaviour's meeting on 'Sex, shopping and sharing: insights from animals to humans and back again' in September 2007. Indeed, a truly integrated discipline would involve the synthesis of not just those researchers working on human behaviour, but all researchers working in the evolutionary behavioural sciences, whatever species they happen to study.

6.1 Applied work

There could be no greater sign of the influence of evolutionary ideas in mainstream biological, social and medical sciences than its use in applied research. There are a number of recent publications by evolutionary researchers attempting to demonstrate the relevance of an evolutionary understanding of human behaviour to policy-making. The first examples include

edited volumes which comprise a range of practical applications of evolutionary theory (Somit and Peterson 2003; Crawford and Salmon 2004), or monographs on specific areas of policy (Thornhill and Palmer 2000; Browne 2002). These largely theoretical publications had limited success. The former appear to have been largely ignored by policy-makers (Google Scholar states that both edited volumes have been cited merely twice since their publication). The latter have been unsuccessful, and heavily criticised, because they lack an integrated approach to their subject (critiqued respectively by Smith *et al.* 2001; Sear 2005). But, the fact that they exist demonstrates a clear interest in engaging with applied research.

A more promising line of applied work is that which is grounded from the beginning in empirical and often integrative work. The following research, focussing on a specific problem and testing it in the field, may prove to be more useful to policy-makers in the long run:

- Curtis et al. (2004) have developed an evolutionarily informed measure of disgust sensitivity and have begun to apply this in studies of hygiene behaviour in the developing world (see also Scott *et al.* 2007)
- A study on the effects of cues of being watched on honesty has already attracted interest from both the commercial and public sector (Bateson *et al.* 2006)
- Gibson and Mace made use of life history theory to analyse the impact of a water development project on the demography of a rural Ethiopian population, which stimulated discussion of the implications of development programmes on health and well-being (Gibson and Mace 2006; and see commentary: Berhane 2006)
- Several more examples of the application of evolutionary ideas to development were recently presented at the session on "Human Behavioral Ecology: Applications to International Development and Public Policy" organised by the Evolutionary Anthropology Section of the American Anthropological Association at the 2005 AAA

annual conference (see: Leonetti *et al.* 2007; Shenk 2007; Tucker and Rende Taylor 2007).

6. Conclusion: The Human Evolutionary Behavioural Sciences

We are optimistic that a synthesis of the human evolutionary behavioural sciences is not only possible, but underway. In recent years most sub-disciplines have taken significant steps towards theoretical integration and have broadened methodological frameworks beyond traditional boundaries. Moreover, integrated studies, while not ubiquitous, are a significant feature of the contemporary literature. This is not to gloss over differences between traditional sub-disciplines, as it must be remembered that each approach is effectively concerned with asking different questions about the evolution of human behaviour – but here lies the strength of an integrated approach; by tackling issues from multiple perspectives a complete understanding can emerge.

Acknowledgements

The LSE Work in Progress group and the UCL Culture Club provided useful discussions on earlier drafts of this paper. We would also like to thank Laura Fortunato and Will Brown for their helpful comments on the manuscript.

References

Allal, N., Sear, R., Prentice, A. M. and Mace, R. (2004): An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 271, 465-470.

Alvard, M. S. (2003): The adaptive nature of culture. *Evolutionary Anthropology*, 12, 136-149.

Atkinson, A. P. and Wheeler, M. (2004): The grain of domains: the evolutionary psychological case against domain general cognition. *Mind & Language*, 19, 147-176.

Aunger, R. (2000): *Darwinizing Culture: the Status of Memetics as a Science*. Oxford: Oxford University Press.

Barkow, J. H., Cosmides, L. and Tooby, J. (1992): *The Adapted Mind*. New York: Oxford Universty Press.

Barrett, H. C. and Behne, T. (2005): Children's understanding of death as the cessation of agency: a test using sleep versus death. *Cognition*, 96, 93-108.

Barrett, L., Dunbar, R. and Lycett, J. (2002): *Human Evolutionary Psychology*. New York: Palgrave.

Bateson, M., Nettle, D. and Roberts, G. (2006): Cues of being watched enhance cooperation in a real world setting. *Biology Letters*, 2, 412-414.

Baudisch, A. and Vaupel, J. (2005): The age patterns of human fertility and mortality: a new, evo-demographic model. Working paper of the Max Planck Institute of Demographic Research, Rostock.

Baum, W. M., Richerson, P. J., Efferson, C. M. and Paciotti, B. M. (2004): Cultural evolution in laboratory microsocieties including traditions of rule giving and rule following. *Evolution and Human Behavior*, 25, 305-326.

Berhane, Y. (2006): Development projects to improve maternal and child health: assessing the impact. *PLoS Medicine*, 3, e192.

Binmore, K. (2005): *Natural Justice*. Oxford: Oxford University Press.

Bird, D. and O'Connell, J. (2006): Behavioral ecology and archaeology. *Journal of Archaeological Research*, 14, 143-188.

Borgerhof Mulder, M., George-Cramer, M., Eshleman, J. and Ortolani, A. (2001): A study of East African kinship and marriage using a phylogenetically based comparative method. *American Anthropologist*, 103, 1059–1082.

Borgerhoff Mulder, M. (1991): Human Behavioural Ecology. In: Krebs, J. R. and Davies, N. B. (eds): *Behavioural Ecology: an Evolutionary Approach*. Oxford: Blackwell Scientific Publications, pp. 69-98.

Borgerhoff Mulder, M. (1998): The Demographic Transition: Are We Any Closer to an Evolutionary Explanation? *Trends in Ecology and Evolution*, 13, 266-270.

Borgerhoff Mulder, M., Nunn, C. L. and Towner, M. C. (2006): Cultural macroevolution and the transmission of traits. *Evolutionary Anthropology*, 15, 52-64.

Bowlby, J. (1969): *Attachment*. London: Hogarth Press.

Bowles, S. and Gintis, H. (2002): The inheritance of inequality. *Journal of Economic Perspectives*, 16, 3-30.

Boyd, R. and Richerson, P., J (1985): *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R. and Richerson, P., J (2005): *The Origin and Evolution of Cultures*. Oxford: Oxford University Press.

Brown, W. M. (2001): Natural selection of mammalian brain components. *Trends in Ecology & Evolution*, 16, 471-473.

Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Liu, C. K., Popovic, Z. and Trivers, R. (2005): Dance reveals asymmetry especially in young men. *Nature*, 438, 1148-1150.

Browne, K. R. (2002): *Biology at Work: Rethinking Sexual Equality*. New Brunswick: Rutgers University Press.

Buller, D. J. (2005): *Adapting Minds: Evolutionary Psychology and the Persistent Quest for Human Nature* Boston, MA: Bradford Books.

Buss, D. M. (1989): Sex differences in human mate preferences: evolutionary hypotheses tested in 37 countries. *Behavioral and Brain Sciences*, 12, 1-49.

Buss, D. M. (1995): Evolutionary psychology: a new paradigm for psychological science. *Psychological Inquiry*, 6, 1-30.

Cassidy, A. (2005): Popular evolutionary psychology in the UK: an unusual case of science in the media? *Public Understanding of Science*, 14, 115-141.

Cassidy, A. (2006): Evolutionary psychology as public science and boundary work. *Public Understanding of Science*, 15, 175-205.

Cavalli-Sforza, L. and Feldman, M. (1981): *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press.

Collard, M., Shennan, S. J. and Tehrani, J. J. (2006): Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evolution and Human Behavior*, 27, 169-184.

Crawford, C. B. (1993): The future of sociobiology: counting babies or studying proximate mechanisms. *Trends in Ecology & Evolution*, 8, 183-186.

Crawford, C. B. and Salmon, C. (2004): *Evolutionary Psychology, Public Policy and Personal Decisions*. New Jersey: Lawrence Erlbaum.

Cronk, L. (1991): Human Behavioural Ecology. *Annual Review of Anthropology*, 20, 25-53.

Cronk, L. (1999): *That Complex Whole: Culture and the Evolution of Human Behavior* London: Westview Press.

Curtis, V., Aunger, R. and Rabie, T. (2004): Evidence that disgust evolved to protect from risk of disease. *Proceedings of the Royal Society B: Biological Sciences*, 271, S131-S133.

Daly, M. and Wilson, M. (2005): Carpe diem: Adaptation and devaluing the future. *Quarterly Review of Biology*, 80, 55-60.

Daly, M. and Wilson, M. I. (1999): Human evolutionary psychology and animal behaviour. *Animal Behaviour*, 57, 509-519.

Davis, J. and Werre, D. (2007): Agonistic stress in early adolescence and its effects on reproductive effort in young adulthood. *Evolution and Human Behavior*, 28, 228-233.

Dennell, R. and Roebroeks, W. (2005): An Asian perspective on early human dispersal from Africa. *Nature*, 438, 1099-1104.

de Winter, W. and Oxnard, C. E. (2001): Evolutionary radiations and convergences in the structural organization of mammalian brains. *Nature*, 409, 710-714.

Dickins, T. E. (2003): What can evolutionary psychology tell us about cognitive architecture? . *History and Philosophy of Psychology*, 5, 1-16.

Dickins, T. E. (2005): On the aims of evolutionary theory: a review of Odling-Smee, J.J., Laland, K.N. and Feldman, M.W. (2003) Niche Construction: the Neglected Process in Evolution. *Evolutionary Psychology*, 3, 79-84.

Dickins, T. E. and Dickins, B. J. A. (2007): Mother nature's tolerant ways: Why non-genetic inheritance has nothing to do with evolution. *New Ideas in Psychology*, doi:10.1016/j.newideapsych.2007.03.004.

Downes, S. M. (2001): Some recent developments in evolutionary approaches to the study of human cognition and behavior. *Biology & Philosophy*, 16, 575-595.

Dunbar, R. I. M. and Barrett, L. (2007a): Evolutionary psychology in the round. In: Dunbar, R. I. M. and Barrett, L. (eds): *The Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press, pp. 3-10.

Dunbar, R. I. M. and Barrett, L. (2007b): *Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press.

Efferson, C., Richerson, P. J., McElreath, R., Lubell, M., Edsten, E., Waring, T. M., Paciotti, B. and Baum, W. (2007): Learning, productivity, and noise: an experimental study of cultural transmission on the Bolivian Altiplano. *Evolution and Human Behavior*, 28, 11-17.

Ellison, P. T. (2001): *Reproductive Ecology and Human Evolution*. New York: Aldine Transaction.

Ellison, P. T. (2003): *On Fertile Ground: A Natural History of Human Reproduction*. Boston: Harvard University Press.

Eriksson, K., Enquist, M. and Ghirlanda, S. (this volume): Critical points in current theory of conformist social learning. *Journal of Evolutionary Psychology*.

Evans, P. D., Gilbert, S. L., Mekel-Bobrov, N., Vallender, E. J., Anderson, J. R., Vaez-Azizi, L. M., Tishkoff, S. A., Hudson, R. R. and Lahn, B. T. (2005): Microcephalin, a gene regulating brain size, continues to evolve adaptively in humans. *Science*, 309, 1717-1720.

Feldman, M. W. and Laland, K. N. (1996): Gene-culture coevolutionary theory. *Trends in Ecology & Evolution*, 11, 453-457.

Fodor, J. (2000): *The Mind Doesn't Work That Way*. Cambridge, MA: MIT Press.

Foley, R. (1995): The adaptive legacy of human evolution: A search for the environment of evolutionary adaptedness. *Evolutionary Anthropology: Issues, News, and Reviews*, 4, 194-203.

Fortunato, L., Holden, C. and Mace, R. (2006): From bridewealth to dowry? A Bayesian estimation of ancestral states of marriage transfers in Indo-European groups. *Human Nature*, 17, 355-376.

Frank, R. H., Gilovich, T. and Regan, D. T. (1993): The evolution of one-shot cooperation: an experiment. *Ethology and Sociobiology*, 14, 247-256.

Freese, J., Li, J.-C. A. and Wade, L. D. (2003): The potential relevances of biology to social enquiry. *Annual Review of Sociology*, 29, 233-256.

Furnham, A., Moutafi, J. and Baguma, P. (2002): A cross-cultural study on the role of weight and waist-to-hip ratio on female attractiveness. *Personality and Individual Differences*, 32, 729-745.

Gangestad, S. W., Haselton, M. G. and Buss, D. M. (2006): Evolutionary foundations of cultural variation: evoked culture and mate preferences. *Psychological Inquiry*, 17, 75-95.

Gangestad, S. W. and Simpson, J. A. (2007a): *The Evolution of Mind: Fundamental Questions and Controversies*. New York: Guildford Press.

Gangestad, S. W. and Simpson, J. A. (2007b): Whither science of the evolution of mind? In: Gangestad, S. W. and Simpson, J. A. (eds): *The Evolution of Mind: Fundamental Questions and Controversies*. New York: Guilford Press, pp. 397-437.

Gibson, M. and Mace, R. (2006): An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia. *PLos Medicine*, 3, e87.

Gigerenzer, G. and Todd, P. M. (1991): *Simple Heuristics That Make Use Smart*. Oxford: Oxford University Press.

Gintis, H. (2000): Classical versus evolutionary game theory - Commentary discussion. *Journal of Consciousness Studies*, 7, 300-304.

Gintis, H., Bowles, S., Boyd, R. and Fehr, E. (2006): *Moral Sentiments and Material Interests: the Foundations of Cooperation in Economic Life*. Boston: MIT Press.

Gould, S. J. and Lewontin, R. C. (1979): The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B*, 205, 581-598.

Grafen, A. (1984): Natural selection, kin selection and group selection. In: Krebs, J. and Davies, N. B. (eds): *Behavioural Ecology: an Evolutionary Approach. 2nd edn*. Oxford: Blackwell Scientific Publications, pp. 62-84.

Gray, R. D., Heaney, M. and Fairhall, S. (2003): Evolutionary Psychology and the challenge of adaptive explanation. In: Sterelny, K. and Fitness, J. (eds): *From Mating to Mentality: Evaluating Evolutionary Psychology*. London & New York: Psychology Press, pp.

Hagen, E. H. (2005): Controversies surrounding evolutionary psychology. In: Buss, D. M. (eds): *The Handbook of Evolutionary Psychology*. New Jersey: John Wiley & Sons, pp. 145-176.

Hagen, E. H. and Barrett, H. C. (2007): Perinatal sadness among Shuar women: support for an evolutionary theory of psychic pain. *Medical Anthropology Quarterly*, 21, 22-40.

Henrich, J. and Boyd, R. (1998): The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19, 215-241.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R., Alvard, M., Barr, A., Ensminger, J., Henrich, N. S., Hill, K., Gil-White, F., Gurven, M., Marlowe, F. W., Patton, J. Q. and Tracer, D. (2005): "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, 28, 795-815.

Henrich, J. and McElreath, R. (2003): The evolution of cultural evolution. *Evolutionary Anthropology*, 12, 123-135.

Heyes, C. (2000): Evolutionary pyschology in the round. In: Heyes, C. and Huber, L. (eds): *Evolution of Cognition*. Cambridge: Cambridge University Press, pp. 3-22.

Hill, A. V. S., Allsop, C. E. M., Kwiatkowski, D., Anstey, N. M., Twumasi, P., Rowe, P. A., Bennett, S., Brewster, D., McMichael, A. J. and Greenwood, B. M. (1991): Common West African HLA antigens are associated with protection from severe malaria. *Nature*, 352, 595-600.

Hill, K. (2007): Evoluitonary biology, cognitive adaptations and human culture. In: Gangestad, S. W. and Simpson, J. A. (eds): *The Evolution of Mind: Fundamental Questions and Controversies*. New York: Guilford Press, pp. 348-356.

Hill, S. E. and Reeve, H. K. (2005): Low fertility in humans as the evolutionary outcome of snowballing resource games. *Behavioural Ecology*, 16, 398-402.

Hobcraft, J. (2006): The ABC of demographic behaviour: How the interplays of alleles, brains, and contexts over the life course should shape research aimed at understanding population processes. *Population Studies*, 60, 153-187.

Holden, C. and Mace, R. (1997): Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology*, 69, 605-628.

Holden, C. and Mace, R. (1999): The sexual division of labour and dimorphism in stature: a phylogenetic cross-cultural analysis. *American Journal of Physical Anthropology*, 110, 27-45.

Hutchinson, J. M. C. and Gigerenzer, G. (2005): Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet. *Behavioural Processes*, 69, 97-124.

Irons, W. (1998): Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evolutionary Anthropology*, 6, 194-204.

Jones, B. C., DeBruine, L. M., Little, A. C., Burriss, R. P. and Feinberg, D. R. (2007): Social transmission of face preferences among humans. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 274, 899-903.

Kanazawa, S. (2004): The Savanna Principle. *Managerial and Decision Economics*, 25, 41-54.

Kaplan, H., Lancaster, J. B., Bock, J. and Johnson, S. (1995a): Fertility and fitness among Albuquerque men: a competitive labour market theory. In: Dunbar, R. I. M. (eds): *Human Reproductive Decisions: Biological and Social Perspectives*. London: Macmillan, pp. 96-136.

Kaplan, H., Lancaster, J. B., Tucker, W. T. and Anderson, K. G. (2002): Evolutionary approach to below replacement fertility. *American Journal of Human Biology*, 14, 233-256.

Kaplan, H. S. and Gangestad, S. W. (2005): Life history theory and evolutionary psychology. In: Buss, D. M. (eds): *Handbook of Evolutionary Psychology*. New Jersey: John Wiley & Sons, pp. 68-95.

Kaplan, H. S., Lancaster, J. B., Bock, J. A. and Johnson, S. E. (1995b): Does observed fertility maximize fitness among New-Mexican men: a test of an optimality model and a new theory of parental investment in the embodied capital of offspring. *Human Nature*, 6, 325-360.

Krebs, J. and Davies, N. (1993): *An Introduction to Behavioural Ecology*. Oxford: Blackwell.

Laland, K. N. and Brown, G. R. (2002): *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour*. Oxford: Oxford University Press.

Laland, K. N. and Brown, G. R. (2006): Niche construction, human behavior and the adaptive-lag hypothesis. *Evolutionary Anthropology*, 15, 95-104.

Lee, R. D. (2003): Rethinking the evolutionary theory of aging: Transfers, not births, shape social species. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 9637-9642.

Leonetti, D., Nath, D. and Hemam, N. (2007): The behavioral ecology of family planning. *Human Nature*, 18, 225-241.

Lewontin, R. C., Rose, S. and Kamin, L. (1984): *Not in Our Genes: Biology, Ideology and Human Nature*. London: Random House.

Lumsden, C. and Wilson, E. (1981): *Genes, Mind and Culture: The Coevolutionary Process*. Cambridge, MA: Havard University Press.

Mace, R. (1998): The coevolution of human wealth and inheritance strategies. *Philosophical Transactions of the Royal Society of London B*, 353, 389-397.

Mace, R. (2007): The evolutionary ecology of human family size. In: Dunbar, R. and Barrett, L. (eds): *The Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press, pp. 383-396.

Mace, R. and Holden, C. (1999): Evolutionary ecology and cross-cultural comparison: the case of matrilineal descent in sub-Saharan Africa. In: Lee, P.C. (ed) *Comparative Primate Socioecology*. Cambridge: Cambridge University Press, pp. 387-405.

Mace, R. and Holden, C. J. (2005): A phylogenetic approach to cultural evolution. *Trends in Ecology & Evolution*, 20, 116-121.

Mameli, M. (2007): Evolution and pyschology in philosophical perspective. In: Dunbar, R. I. M. and Barrett, L. (eds): *The Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press, pp. 21-34.

McElreath, R. (2004): Social learning and the maintenance of cultural variation: An evolutionary model and data from east Africa. *American Anthropologist*, 106, 308-321.

McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. and Paciotti, B. (2005): Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, 26, 483-508.

McNamara, J. M. and Houston, A. I. (2006): State and Value: A Perspective from Behavioural Ecology. In: Wells, J. C. K., Strickland, S. S. and Laland, K., N (eds): *Social Information Transmission and Human Biology* 59-88.

Mekel-Bobrov, N., Gilbert, S. L., Evans, P. D., Vallender, E. J., Anderson, J. R., Hudson, R. R., Tishkoff, S. A. and Lahn, B. T. (2005): Ongoing adaptive evolution of ASPM, a brain size determinant in Homo sapiens. *Science*, 309, 1720-1722.

Menzel, R. and Giurfa, M. (2001): Cognitive architecture of a mini-brain: the honeybee. *Trends in Cognitive Sciences*, 5, 62-71.

Mesoudi, A. (2007): Using the methods of experimental social psychology to study cultural evolution. *Journal of Social, Cultural and Evolutionary Psychology*, 1, 35-58.

Mesoudi, A., Whiten, A. and Dunbar, R. (2006): A bias for social information in human cultural transmission. *British Journal of Psychology*, 97, 405-423.

Moore, F. R. and Cassidy, C. (2007): Female status predicts female mate preferences across nonindustrial societies. *Cross-Cultural Research*, 41, 66-74.

Murphy, M. (1999): Is the relationship between fertility of parents and children really weak? *Social Biology*, 46, 122-145.

Nesse, R. M. and Williams, G. C. (1995): *Evolution and Healing: New Science of Darwinian Medicine*. Phoenix Press.

Nettle, D. (2007): Individual differences. In: Dunbar, R. I. M. and Barrett, L. (eds): *The Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press, pp. 479-490.

Newson, L., Postmes, T., Lea, S. E. G., Webley, P., Richerson, P., J and McElreath, R. (2007): Influences on communication about reproduction: the cultural evolution of low fertility. *Evolution and Human Behavior*, 23, 199-210.

O'Brien, M. J. and Lyman, R. L. (2002): Evolutionary archeology: Current status and future prospects. *Evolutionary Anthropology*, 11, 26-36.

Parker, G. A. and Maynard Smith, J. (1990): Optimality theory in evolutionary biology. *Nature*, 348, 27-33.

Perrusse, D. (1993): Cultural and reproductive success in idustrial societies: Testing the relationship at the proximate and ultimate levels. *Brain and Behavioral Sciences*, 16, 267-323.

Potts, R. (1998): Variability selection in hominid evolution. *Evolutionary Anthropology*, 7, 81-96.

Richerson, P., J and Boyd, R. (2005): *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.

Rose, H., Rose, S. and Jencks, C. (2000): *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*. London: Harmony Books.

Samuels, R. (1998): Evolutionary psychology and the massive modularity hypothesis. *British Journal of Philosophical Science*, 49, 575-602.

Samuels, R. (2000): Massively modular minds: the evolutionary psychology account of cognitive architecture. In: Carruthers, P. and Chamberlain, A. (eds): *Evolution and the Human Mind: Modularity, Language and Meta-cognition*. Cambridge: Cambridge University Press, pp. 13-46.

Scott, B. E., Lawson, D. W. and Curtis, V. (2007): Hard to handle: understanding mothers' handwashing behaviour in Ghana. *Health Policy and Planning*, 22, 216-224.

Sear, R. (2005): Review of Biology at Work: Rethinking Sexual Equality. *Sexualities, Evolution and Gender*, 7, 189-193.

Segerstråle, U. (2000): *Defenders of the Truth: The Sociobiology Debate*. Oxford: Oxford University Press.

Shenk, M. (2007): Dowry and public policy in contemporary India. *Human Nature*, 18, 242-263.

Sherman, P. W. and Reeve, H. K. (1997): Forward and backward: alternative approaches to studying human social evolution. In: Betzig, L. (eds): *Human Nature: A Critical Reader*. Oxford: Oxford University Press, pp. 147-158.

Smith, E. A. (2000): Three styles in the evolutionary analysis of human behaviour. In: Cronk, L., Chagnon, N. and Irons, W. (eds): *Adaptation and Human Behaviour: an Anthropological Perspective*. New York: Aldine de Gruyter, pp. 27-47.

Smith, E. A., Borgerhoff Mulder, M. and Hill, K. (2000): Evolutionary analyses of human behaviour: a commentary on Daly & Wilson. *Animal Behaviour*, 60, F21-F26.

Smith, E. A., Borgerhoff Mulder, M. and Hill, K. (2001): Controversies in the evolutionary social sciences: a guide for the perplexed. *Trends in Ecology and Evolution*, 16, 128-135.

Somit, A. and Peterson, S. (2003): *Human Nature and Public Policy: an Evolutionary Approach*. New York: Palgrave Macmillan.

Strassmann, B. I. and Dunbar, R. I. M. (1999): Human evolution and disease: putting the stone age in perspective. In: Stearns, S. C. (eds): *Evolution in Health and Disease*. Oxford: Oxford University Press, pp. 91-101.

Swami, V., Caprario, C., Tovée, M. J. and Furnham, A. (2006): Female physical attractiveness in Britain and Japan: a cross-cultural study. *European Journal of Personality*, 20, 69-81.

Swami, V. and Tovee, M. J. (2007): Perceptions of female body weight and shape among indigenous and urban Europeans. *Scandinavian Journal of Psychology*, 48, 43-50.

Symons, D. (1989): A critique of Darwinian anthropology. *Ethology and Sociobiology*, 10, 131-144.

Symons, D. (1992): On the use and misuse of Darwinism in the study of human behaviour. In: Barkow, J. H., Cosmides, L. and Tooby, J. (eds): *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press, pp. 137-159.

Thornhill, R. and Palmer, C. T. (2000): *A Natural History of Rape: Biological Bases of Sexual Coercion*. Cambridge, MA: MIT Press.

Tooby, J. and Cosmides, L. (1992): The psychological foundations of culture. In: Barkow, J. H., Cosmides, L. and Tooby, J. (eds): *The Adapted Mind*. New York: Oxford Universty Press, pp. 19-136.

Tovee, M. J., Swami, V., Furnham, A. and Mangalparsad, R. (2006): Changing perceptions of attractiveness as observers are exposed to a different culture. *Evolution and Human Behavior*, 27, 443-456.

Tucker, B. and Rende Taylor, L. (2007): The human behavioral ecology of contemporary world issues. *Human Nature*, 18, 181-189.

Vining, D. R. J. (1986): Social versus reproductive success: the central theoretical problem of human sociobiology. *Behaviour and Brain Sciences*, 9, 167-216.

Waynforth, D. (2007): Mate choice copying in humans. *Human Nature*, 18, 264-271.

West-Eberhard, M. J. (2003): *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

White, D. W., Dill, L. M. and Crawford, C. B. (2007): A common, conceptual framework for behavioral ecology and evolutionary psychology. *Evolutionary Psychology*, 5, 275-288.

Williamson, S., Hubisz, M., Clark, A., Payseur, B., Bustamante, C. and Nielsen, R. (2007): Localizing Recent Adaptive Evolution in the Human Genome. *Plos Genetics*, 3 (6): e90. doi: 10.1371/journal.pgen.0030090.

Wilson, E. O. (1975): *Sociobiology: The New Synthesis*. Cambridge, MA: Belknap Press.

Winterhalder, B. and Smith, E. A. (2000): Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology*, 9, 51-72.

Table 1: Examples of articles reviewing or synthesising evolutionary analyses of human behaviour

Authors	Year	Title	Source	Discipline of authors[7]
Crawford	1993	The future of sociobiology: counting babies or studying proximate mechanisms	Trends in Ecology and Evolution	EP
Sherman & Reeve	1997	Forward and backward: alternative approaches to studying human social evolution	Human Nature: A Critical Reader	Behavioural ecology (BE)
Daly & Wilson	1999	Human evolutionary psychology and animal behaviour	Animal Behaviour	EP
Heyes	2000	Evolutionary psychology in the round	Evolution of Cognition	Animal cognition
Smith, Borgerhoff Mulder & Hill	2000	Evolutionary analyses of human behaviour: a commentary on Daly & Wilson	Animal Behaviour	HBE
Smith	2000	Three styles in the evolutionary analysis of human behaviour	Adaptation and Human Behaviour	HBE
Smith, Borgerhoff Mulder & Hill	2001	Controversies in the evolutionary social sciences: a guide for the perplexed	TREE	HBE
Downes	2001	Some recent developments in evolutionary approaches to the study of human cognition and behavior	Biology & Philosophy	Philosophy
Laland & Brown	2002	Sense and Nonsense		CE & BE
Barrett, Dunbar & Lycett	2002	Chapter 1: The evolutionary approach to human behaviour	Human Evolutionary Psychology	EP
Kaplan & Gangestad	2005	Life history theory and evolutionary psychology	Handbook of Evolutionary Psychology	HBE & EP
Hutchinson & Gigerenzer	2005	Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet	Behavioural Processes	BE & Psychology
Dunbar & Barrett	2007	Evolutionary psychology in the round	Oxford Handbook of Evolutionary Psychology	EP
Gangestad & Simpson	2007	Whither science of the evolution of the mind?	Evolution of the Mind	EP
White, Dill & Crawford	2007	A common, conceptual framework for behavioral ecology and evolutionary psychology	Evolutionary Psychology	BE, EP

[7] Note that these are our own categorisations of the authors' disciplines