

Human Behavioural Ecology

Monique Borgerhoff Mulder, *University of California at Davis, Davis, California, USA*

Ryan Schacht, *University of California at Davis, Davis, California, USA*

Advanced article

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Human behavioural ecology emerged in the mid-1970s as a result of applying the theory of evolution by natural selection to the study of human behaviour. Using explicit models to derive hypotheses that are tested with quantitative data primarily drawn from traditional human communities, it offers a natural science of sociocultural diversity. Recent activity in this field lies in the study of the family, in life history theory and in individual and collective interests, and increasingly the field of enquiry moves from traditional communities to modern industrial societies. Current challenges include incorporating the mechanisms underlying adaptive behaviour, and the developmental and historical causes of human behavioural variability.

Optimality and Human Behaviour

Human behavioural ecology (HBE) can be defined as the evolutionary ecology of human behaviour. It focuses on the analysis of human behavioural variability within the framework of evolutionary theory. The field has grown rapidly over the last 30 years, in anthropology and other social and behavioural sciences. It passes under many names, including Darwinian (or evolutionary) anthropology, human evolutionary ecology, evolutionary biological anthropology, human ethology, socioecology, biosocial (or biocultural) anthropology and sociobiology. Most researchers generally shun using the controversial term sociobiology for three reasons: the inaccurate equation of sociobiology with kin selection (which is but one of its models), the general but erroneous view that sociobiologists see behaviour as genetically determined, and the wish to distance themselves from popular but highly

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speculative and often controversial works under that label (Laland and Brown, 2011).

Behavioural ecology (including HBE) sprang from a growing emphasis within evolutionary biology and animal behaviour throughout the 1960s and 1970s on individual level selection. Already by 1956 the British evolutionary biologist JBS Haldane had argued that behavioural differences could be analysed as the responses of human beings with basically similar genetic compositions to varying natural and sociocultural environments. This idea was developed and given prominence by EO Wilson's (1975) path-breaking book *Sociobiology: The New Synthesis*, in what turned out to be an inflammatory last chapter on humans. Beginning as an embattled group of advocates strongly committed to exploring the relevance for humans of the ideas of prominent biologists such as Richard Alexander, Eric Charnov, William D Hamilton, John Maynard Smith, Gordon Orians, Robert Trivers, George Williams and Edward Wilson, HBE has now established itself by successfully adapting evolutionary ecology theory and methods to a wide range of topics important to anthropology and archaeology (Winterhalder and Smith, 2000). It is represented by societies such as the Human Behavior and Evolution Society, the European Human Behaviour and Evolution Association and the Evolutionary Anthropology Section at the American Anthropological Association, by journals including *Evolution and Human Behavior* and *Human Nature*, and by various book series. **See also:** [Behavioural Ecology](#)

Assumptions and Models

The principal assumption of HBE is that people are selected to respond flexibly to environmental conditions in ways that enhance their fitness. Critical here is the idea that a history of natural selection endows our species with the ability to weigh the costs and benefits of adopting particular strategies, and that these decision rules (and the cognitive and physiological machinery behind them) are the focus of selection. As such HBE frames the study of adaptive design in terms of decision rules, for example, in context X do A and in context Y do B, such that

behavioural variation arises as people match their conditional strategies to their particular circumstances. Accordingly, large differences in behaviour among individuals with no correlated genetic differences can result from varying socioecological opportunities and constraints, as in many other species studied by behavioural ecologists. Furthermore, humans can use culturally transmitted information to adjust their behaviour, through imitation, social learning or other processes. Since fitness is difficult to measure, proximate outcomes (reproductive success, food income or social status) may be used as proxy measures, bringing evolutionary models quite close to quantitative models developed in microeconomics, demography and some schools within sociology and anthropology. A key assumption of this highly adaptationist approach emphasising the current utility of traits is the phenotypic gambit, which is the claim that how a trait is inherited does not seriously constrain adaptive responses to ecological variation. In other words behavioural ecologists assume phenotypic plasticity, and a human ability to assess payoffs and/or learn from others the best alternative under a given set of ecological and social circumstances. This position recognises that behavioural diversity results from the strategic considerations of individuals, from characteristics of the ecological niche, and from the cultural transmission of information (Smith, 2011). **See also:** [Cultural Transmission and Evolution](#)

HBE derives testable hypotheses from either graphical or mathematically explicit models anchored in basic principles of evolution by natural selection. To achieve generality these models seek to identify the bare essentials of an adaptive problem. They are therefore particularly useful in highlighting the key trade-offs that individuals face, for example, between increasing the number of offspring born or ensuring the survival and quality of those already existing (optimal clutch size model; Meij *et al.*, 2009). These models are drawn specifically from optimal foraging, life history, sexual selection and sex allocation theory. They predict optimal behavioural strategies given certain critical constraints and conditions. Where predictions are not met, the assumptions, constraints or applicability of the model itself must be re-evaluated. With increasing sophistication optimality models can incorporate the behaviour of other optimising individuals (game theoretical models), as well as the consequences of previous optimising decisions (dynamic state models), and can use simulations to estimate the payoffs associated with interacting agents or interdependent decisions (Winterhalder, 2002). **See also:** [Natural Selection: Introduction](#)

The assumptions and models outlined above have generated a productive research tradition through analyses of foraging and food production, food sharing, territoriality and spatial use, reproduction, marriage, family organisation and intergenerational inheritance, generating specific hypotheses to explain variation both within and between different human societies. To date most empirical work has been done in contemporary so-called traditional societies, ones only marginally affected by globalisation, where

customary behavioural and subsistence patterns are still maintained and where modern contraception technology is largely absent. Increasingly however, useful studies are conducted in historical populations (e.g. Pollet and Nettle, 2008) and reviews incorporate evidence from modern and ancient societies (Hrady, 1999).

Foraging

Initial explorations of HBE were in the field of foraging (hunter-gatherer) subsistence behaviour, drawing explicitly from optimal foraging theory (OFT). This was in part because OFT was already quite sophisticated and testable by the early 1980s, and in part because so much of the history of our species was spent as foragers. Contemporary foragers offer natural experiments for human behavioural variability. Whereas foragers certainly do not live in environments identical to those in which humans evolved, HBE can use within and between variations in foraging patterns to uncover features of how our species may have adapted to ecological and social changes over time (Winterhalder, 2002). **See also:** [Decision-making and Neuroeconomics](#)

Optimal foraging theory consists of a family of models addressing resource selection, time allocation and habitat movement (patch choice), with the diet breadth (or prey choice) model the most widely used in human studies. In accordance with this model, human foragers are shown in general to select food resources that maximise mean rate of nutrient acquisition (i.e. calories) by trading off the search and handling times associated with prey species of varying profitability. Foragers routinely bypass resources yielding relatively low postencounter return rates when encounters with more profitable items are common, but take a broader array of prey when those items are rare (Kaplan and Hill, 1992). Specific applications explain shifts in subsistence patterns over time in response to such factors as changes in technology, climatic fluctuations and the availability of imported substitutes. For example, the adoption of pursuit-enhancing technologies such as rifles and shotguns by Cree hunter-gatherers in the Canadian north caused diet breadth to expand whereas search-enhancing snowmobiles caused it to contract (Winterhalder, 1981). There are also applications to archaeological remains. For example, deposits associated with communities on the brink of adopting agriculture show increasing exploitation of locally abundant but previously unused resources, notably seeds and other plant food that require extensive processing (Winterhalder and Goland, 1997). As such the diet breadth model suggests that agriculture emerged (many times) in response to lower encounter rates with higher-ranked food items and lower economic efficiency generally, which may itself have resulted from terminal Pleistocene climatic change, human population increase and human-induced habitat change (Richerson *et al.*, 2001). Finally, OFT can be extended to examine the dynamics of horticultural, pastoral and aquatic production systems, such as

reasons why governmental and NGO conservation and poverty alleviation methods fail, how information sharing affects search patterns in modern fisheries and why livestock domestication occurred. In these areas HBE converges closely with microeconomic theory used by game managers, behavioural economists and others (Tucker, 2007).

Failures to support model predictions can be just as enlightening as the successes. For example, despite the broad convergence of foraging behaviour with maximising nutrient acquisition, men sometimes favour large animal prey, ignoring plant food and other smaller game species that are profitable enough to increase their mean acquisition rates, and women do just the opposite, taking plants and other small predictable prey rather than large animals. These observations have generated two competing hypotheses. The first attributes the discrepancies to nutritional needs and/or foraging constraints – that men maximise nutrient gain by paying attention to a currency that gives higher weight to macronutrients (particularly lipids) than to kilocalories, or that women are constrained by child care (Hill, 1988). The second proposes that men favour prey items that are large and irregularly obtained, thus providing windfall resources that have value for the prestige they bring and consequential attraction of many claimants (Hawkes and Bliege Bird, 2002). This latter hypothesis presents an alternative to the long-standing view that men hunt primarily to provision their wives and offspring, and suggests men hunt to attract mates and political allies. Debates such as this remain unresolved, but are tightly linked to the analysis and interpretation of empirical data (Gurven and Hill, 2009). More generally they demonstrate how an HBE perspective integrates topics that are typically somewhat distinct in conventional anthropology – subsistence, marriage, reciprocity, kinship, demography, politics, ritual and health – into a unified theoretical enquiry.

Interesting extensions have emerged from applying foraging models to humans, such as in the field of conservation biology. The picture of traditional communities living in ecological harmony with their environments and protecting their resources from over-exploitation has faded when assessed against behavioural ecology. Because OFT models identify precisely the behaviours expected by short-term optimisation, they provide the null hypothesis against which such a traditional ‘conservation ethic’ can be evaluated. The evidence shows that for the most part traditional foragers select prey species in accordance with the predictions of shorter-term optimisation models, irrespective of the vulnerability of these species to local depletion (Alvard, 1998). **See also:** [Conservation Biology and Biodiversity](#)

Marriage and Raising Offspring

An early and enduring focus in HBE is why human communities exhibit such variable culturally sanctioned mating

patterns, formalised as marriage rules and marital payments. Given consistent evidence from historical and traditional societies that an individual’s access to or control of resources, both material and symbolic (e.g. prestige), positively affects his or her reproductive success, resource-based models were adapted from the avian and mammalian literature to generate predictions from sexual selection theory about how resource distributions affect optimal short- and long-term strategies of men and women. A general finding is that polygyny occurs where men can monopolise resources critical to women’s survival and reproduction. The mechanism here is the choice that women, or their parents on their behalf, make between a wealthy married man and a poorer bachelor, a dilemma formalised in the polygyny threshold model. For example, among the Kipsigis of Kenya women must make decisions regarding prospective husbands both on the resources he holds and the number of wives he currently has. Although there are costs associated with being a co-wife (decreased reproductive success due to competition for resources), if a man has sufficient resources these costs can be offset. In this way, a wealthy man with multiple wives may be a more attractive marriage partner than a poor man with no wives (Borgerhoff Mulder, 1990). Making some coarse generalisations about the relatively homogenous social groups that characterise the ethnographic record, in pastoral herding societies marriage is typically polygynous, with men competing over multiple wives through the transfer of bridewealth payments to the brides’ kin. In farming societies, and particularly where land is scarce, marriage is more typically monogamous and payments often entail dowry, a form of competition among women to be married by the wealthiest men and reject co-wives; where land is plentiful, however, polygyny prevails. Finally, in materially inhospitable environments such as the Himalayas, high male labour inputs into subsistence encourage a younger brother to join his elder brother’s marriage as a secondary husband (polyandry) rather than strive for a monogamous but low success marriage on his own (Kaplan *et al.*, 2009). In all of these cases marital decisions can be modelled as a trade-off between constrained options. Increasingly too it is recognised that the interests of the sexes do not necessarily coincide (Borgerhoff Mulder and Rauch, 2009).

See also: [Sexual Selection and Life History Allocation](#)

Such models have been very productive in linking marriage patterns to salient features of the environment. They also offer an explanatory framework for the very different patterns of intergenerational transmission of material or status resources seen across different societies. Thus polygyny often is associated with patriliney and the inheritance of material wealth to sons (who can turn this inheritance into plentiful grandchildren through their own polygynous marriages), whereas monogamy is, at least in stratified societies, associated with dowry payments to daughters, facilitating upward mobility for girls and potentially greater returns with respect to grandparental fitness (Kaplan *et al.*, 2009). Matrilineal inheritance is often found where the certainty of paternity is low and where there are

few heritable resources that could benefit sons over daughters (Figure 1).

Closely related and equally interesting are patterns of parental investment. Human offspring require extensive and extended parental care, beginning *in utero* and ending in some cases as late as the execution of a will or other mechanisms of inheritance (Hrdy, 1999). This investment affects a child's health, survival, future mating success and hence the parent's inclusive fitness (own fitness plus effects of its action on fitness of relatives weighted by their average relatedness). **See also:** [Fitness](#)

Considerable attention has been given to the adaptive reasons for differential investment in offspring. Parental fitness payoffs depend on three sets of factors: (1) the genealogical relatedness between caregiver and child; (2) the effect of investment on the reproductive value of the child (their expected future reproductive output) and (3) the effects of caregiving on the caregiver's own reproductive value, which can be thought of as an opportunity cost to the investor. Whereas all these factors likely influence parental strategies, to date, simple models have been adopted from non-HBE that identify certain key variables that might bias parental investment in offspring, for the most part testing them separately or in small combinations. Many of the evolutionary predictions about parental investment have been supported (Winterhalder and Smith, 2000), for example, step children often receive less investment than biological children (Daly and Wilson, 1985). Similarly parental investment theory more accurately predicts which children end up as sex workers in

contemporary northern Thailand than do predictions derived from poverty levels alone (Rende Taylor, 2005).

Life History Allocations

The adaptive trade-offs at the core of life history theory are central to HBE. Organisms face two major energy allocation decisions, the first between growth and reproduction, and the second between the number of offspring produced and the amount to be invested in each. As such, life history studies are concerned with the evolution of maturation rates, reproductive rates and timing, dispersal patterns, mortality patterns and senescence. A highly influential early study used David Lack's optimal clutch size model to show how the Kung San birth interval of 4 years is optimal with respect to the production of surviving offspring in the harsh Kalahari environment (Blurton Jones, 1986). Subsequent analyses of variation in hunter-gatherer fertility levels lend some support to the hypothesis that variations in fertility reflect the costs of child rearing, which are themselves a consequence of the character and distribution of resources and associated age- and sex-specific foraging practices. Furthermore in African horticulturalists there is some evidence to suggest that women produce an optimal clutch size, meaning that higher fertility would produce fewer surviving children (Figure 2).

See also: [Life History Theory](#)

One life history trade-off that has drawn particular attention is age at first reproduction which varies widely

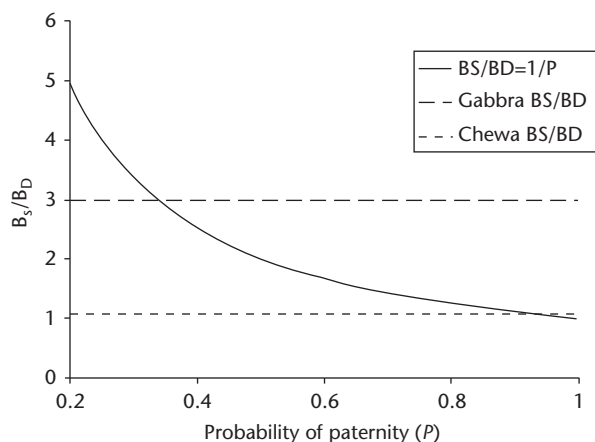


Figure 1 Direction of parental sex-bias. The vertical axis shows the ratio of the benefit of inherited wealth to sons (BS) and daughters (BD). The horizontal axis shows the probability of paternity (P). The solid black line $BS/BD=1/P$ shows when it is equally adaptive to invest in sons' and daughters' children. For values above this line, it is adaptive to invest in sons; for values below this line, it is adaptive to invest in daughters. Broken lines show empirically derived values of BS/BD for two African societies, the Gabbra (dotted line) and Chewa (dashed line). The point where these lines cross the solid line ($BS/BD=1/P$) shows the critical value of P needed to make daughter biased wealth inheritance adaptive in that society ($P < 0.36$ in the Gabbra, $P < 0.94$ in the Chewa). Adapted with permission from Holden C, Sear R and Mace R (2003) Matriliney as daughter-biased investment. *Evolution and Human Behavior* 24: 99–112. Copyright by Elsevier.

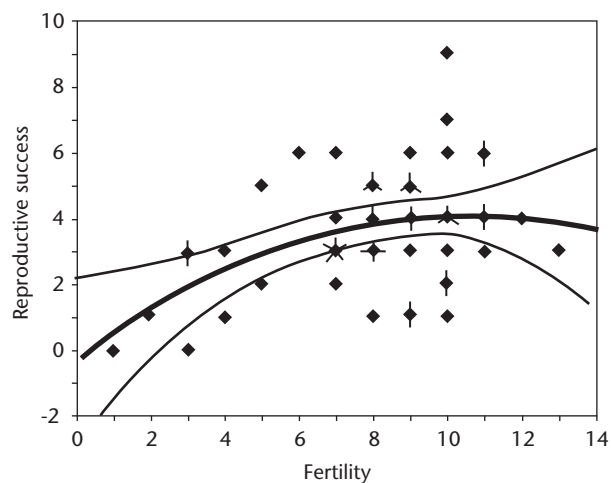


Figure 2 The relationship between fertility and reproductive success. According to life-history theory, an organism that maximises fitness will face a trade-off between female fertility and offspring survivorship. These data from the Dogon of Mali (West Africa, $n = 55$ women) show the predicted nonlinear relationship between women's fertility and reproductive success. Reproductive success is measured as survival to age 10, and each 'petal' on a data point represents an additional case; the regression line in bold is shown with 95% confidence limits. Adapted with permission from Strassmann BI and Gillespie B (2002) Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society of London. Series B* 269: 553–562. Copyright by The Royal Society.

across and between populations (Volland, 1998). The age at which women start sexual activity or have their first child is predicted by life history models to be highly sensitive to variation in mortality rates (if chances of survival are low, start early) and the productivity of nonreproductive activities (if you can efficiently accrue resources useful to reproduction, delay). A large number of studies support one or both of these relationships, an evolutionary response that may be shaped by early developmental conditions (Nettle, 2011). Low *et al.* (2008), for example, found a positive relationship between life expectancy at birth and age at first birth across societies of varying economic development (Figure 3). More generally, perhaps the most successful study to date of the dilemma of allocation between growth and reproduction is that of Hill and Hurtado (1996) who examine, from a life history perspective, patterns of growth, fertility and mortality in a precontact foraging population through painstaking reconstruction. They adapt a life history model of reproductive timing to successfully predict variation in age of

reproductive maturation of women in three different populations, ranging from foragers to urban industrial North Americans.

Comparing human life histories to those of other primates and mammals reveals at least four distinctive characteristics of our species: a very large brain, an exceptionally long lifespan, an extended period of juvenile dependence, and support of reproduction by older post-reproductive individuals. A more controversial fifth feature is men's support of reproduction through the provisioning of women and their offspring. Attempts to link these features through a behavioural ecological analysis have generated two co-evolutionary narratives. These five traits may be coevolved adaptive responses to a dietary shift towards high-quality, nutrient-dense and difficult-to-acquire food resources which occurred only with the emergence of our species (Kaplan, 1996). The alternative is the grandmother hypothesis (Hawkes, 2003). In this second scenario, the appearance of arid seasonal environments 1.7–1.8 million years ago put pressure on *Homo ergaster*

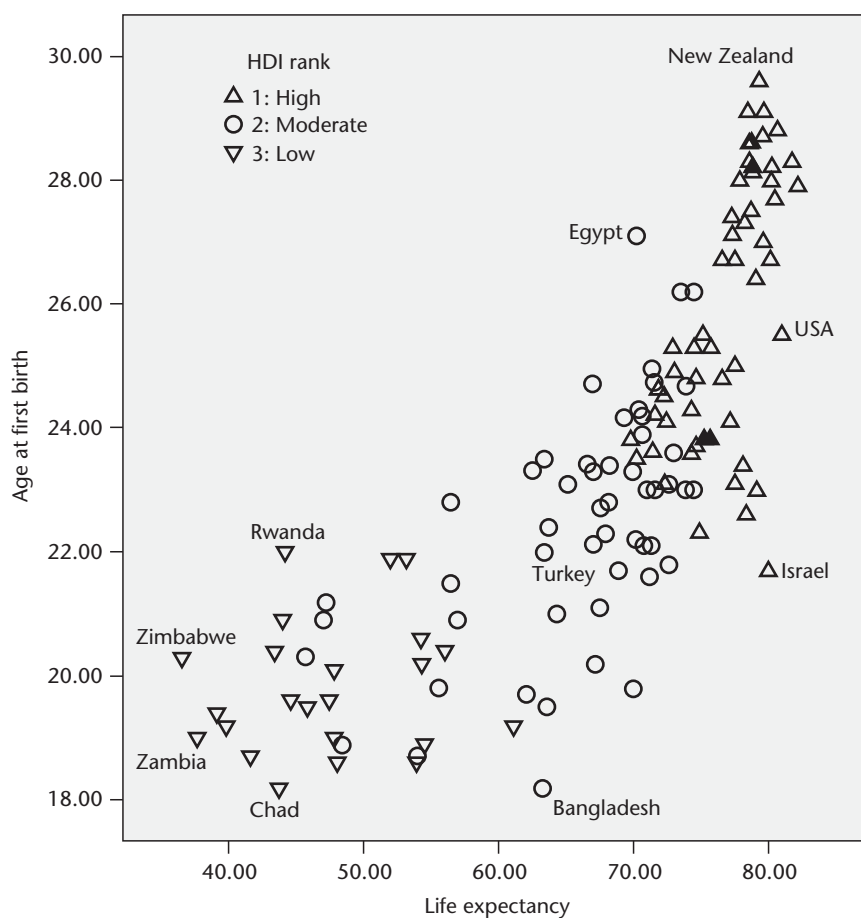


Figure 3 Women's age at first birth increases nonlinearly with life expectancy at birth (Smoothing Spline Fit, $\lambda=2000$; $R^2=0.677$). Countries are denoted by their Human Development Index (HDI) rank (a complex measure of quality of life). The association between life expectancy and age at first birth is positive and statistically significant within all three HDI ranks, although high, moderate and low human development countries occupy different parts of the curve. The pattern among countries with high HDI rank (Norway, United States, Japan, etc.) suggests a relatively strong relationship between life expectancy and age at first birth within the most developed nations. Adapted with permission from Low *et al.* (2008). Copyright by Sage Publications.

mothers to find new sources of food to feed themselves and their offspring. To obtain sufficient food they turned to low-ranked food resources such as tubers that were widespread but demanded adult strength to harvest, and thus more work for the mother. According to the grandmother hypothesis, this constraint provided an opportunity for ageing female relatives to offset the declines in their own fitness by stepping in to provision grandchildren, thus selecting for a post-reproductive lifespan. The debate between these narratives has broadened into a more general focus on humans as cooperative breeders due to alloparental assistance by both kin and non-kin (Hrdy, 2009) with increasing interest in empirical evidence on the range of kin who assist with the raising of offspring (Sear and Mace, 2008). Even though there is strong evidence that grandmothers can be helpful in some contexts, such as the nineteenth rural populations of European descent (Lahdenperä *et al.*, 2004), other studies demonstrate that fathers are important contributors to child welfare, as in the Tsimane horticulturalists of Bolivia (Winkling *et al.*, 2007). **See also:** [The Evolution and Ecology of Cooperative Breeding in Vertebrates](#)

As in most other areas of HBE inquiry, simple models have sparked interest not only just in the past but also in the present. An example here is the study of the dramatic decline in fertility, known as the demographic transition that has been occurring across the world over the last 150 years, as they gradually became richer (Borgerhoff Mulder, 1998). Specifically, the relatively affluent reduced their family size before such comparable adjustments among the poor. This has been taken by some critics of HBE as evidence that humans do not behave in ways that are adaptive, and that they do not consistently use resources to augment their fitness. This critique nicely exemplifies some common misconceptions about an evolutionary approach – that all behaviour should be adaptive, that only panhuman patterns are evidence of evolved behaviour and that models supported in nonhuman systems (e.g. strong correlations between dominance and reproductive success) should necessarily also be evidenced in humans.

In fact the disruption of the common association between rank, wealth and fitness that is observed in different societies at different times over the recent demographic transition challenges HBE to examine more carefully the environmental, social and physiological factors that influence optimal fitness-maximising strategies. A key idea here is that rather than maximising the number of offspring raised, humans adjust fertility in ways that maximise longer-term fitness. This latter can be measured as the number of grandchildren, or in more complex analyses as a weighted product of children and wealth, a fertility function adjusted by risk or a simulated function. These explanations build on the trade-off between offspring quality and offspring quantity, highlighting the possibility that particularly high levels of offspring quality are required in societies dominated by labour markets that reward human capital. Without analyses of the long-term fitness consequences of a variety of different fertility

strategies in different kinds of environments, it is probably still premature to conclude that the low current levels of fertility in much of the developed world are maladaptive. Nevertheless this area of research represents one of the most integrative lines of enquiry to emerge from HBE (Lawson *et al.*, in press).

Individual and Collective Interests

Almost invariably humans belong to groups – families, broader kinship groups, villages, lineages, communities, tribes and nations, groups that may (or may not) be residential and may (or may not) be inclusive of each other. Some of these groupings are relatively egalitarian in organisation, whereas others are stratified, with certain individuals enjoying more power or prestige than others. The individual selectionist perspective of behavioural ecology highlights the conflict of interests among individuals at each level as well as the potential for cooperation within and between groups, as do some schools within economics, political science and sociology. As such, it explores the inherent costs and benefits entailed in group living, and the implications of these costs and benefits for the emergence of sociopolitical hierarchies (Boone, 1992). A behavioural ecological approach suggests intriguing ideas that may have relevance for higher levels of social organisation.

The first is food sharing. At present, most of the hypothesis development for human sociality has centred on resource transfers within foraging groups, usually measured as food sharing. Commonly human foragers take at least some resources that are larger than the harvester can consume, for example, a medium-sized ungulate. Furthermore, if only one member of the group has been successful in the hunt and others come back empty-handed, portions of the packet will be differently valued by different group members, depending on how hungry they are. A large number of hypotheses addressing the evolutionary mechanisms that maintain food sharing have been proposed, and current evidence strongly suggests that in different circumstances different mechanisms may be important (Gurven, 2004). Thus individuals in control of a food resource may share it to provision their kin, to trade the resource for another valued scarce item, to ensure (through reciprocity) against the risk of being without food at some future point in time when hunting was unsuccessful, or to advertise quality or seek attention among those who have been unable to procure resources (a signalling hypothesis where the benefits may perhaps be reaped through sexual selection). There is considerable potential for exploring these ideas more generally through modelling. For example, individuals are most likely to cede resources to others, for example, where the costs of ownership and fighting contests are high, where the returns to holding resources are nonlinear and where individuals' fates are independent (Nettle *et al.*, 2011).

The second is cooperation. Despite the predictions of narrowly self-interested behaviour predicated on the ultimately competitive nature of selection, humans for the most part live in stable cooperative groups, and come together to produce valuable collective goods – goods that could not be produced as effectively by one or a few individuals (economies of scale). Indeed this is probably one of the hallmarks of being human, shared only with the eusocial insects. Kin selection and reciprocity are commonly invoked as solutions to cooperative dilemmas, but many human groups, even those of our foraging ancestors, are made up of non-kin and reciprocity is always vulnerable to cheaters. There have been many recent game theoretical attempts to address this problem, but one particularly fruitful empirical line of research lies in the field of experimental economics. Behavioural ecologists and others, administering experiments in many different cultural contexts, are finding that people often cooperate in anonymous one-shot games where noncooperation would lead to a higher payoff for any individual player but cooperation leads to highest mean payoff for all the players. Furthermore engagement in large-scale institutions such as markets, is associated with greater fairness, as measured by an individual's contribution to an anonymous co-player made in the dictator game across 15 different communities (Figure 4). These findings suggest not only that models based on short-term material self-interest may need to be seriously revised when dealing with human sociality, but also that new social norms and informal institutions may have emerged in our species to support social interaction in ever-widening socioeconomic spheres with non-kin and

strangers (Chapais, 2008). They also point to possible importance of cultural group selection in contributing to human success, insofar as groups characterised by stable patterns of cooperation may well have outcompeted groups with more individualistic tendencies.

Conceptual Challenges

Evolutionary studies of behaviour ideally incorporate investigations of mechanism, development and phylogeny, as well as those of functional (or adaptive) significance. The focus of behavioural ecology (both human and other) is principally on function, and the environmental factors that shape variations in behaviour through the process of optimisation. Less attention has been paid (until recently) to the precise mechanistic, developmental or historical causes of variation. Indeed, the phenotypic gambit is invoked broadly to suggest that not only genetic, but also phylogenetic and cognitive mechanisms do not seriously constrain human adaptive responses to ecological variation. In other words a behavioural ecologist predicts a certain matching between behavioural strategy and context (as defined in formal models) irrespective of whether humans reach this adaptive strategy as a consequence of genes, psychological mechanism or the learning of culture. As such, this gambit is getting increasing attention, stimulating some truly novel developments that can only enrich the field insofar as behavioural ecology becomes more attuned to the special challenge of explaining what may be uniquely human (music, religion, language, etc.).

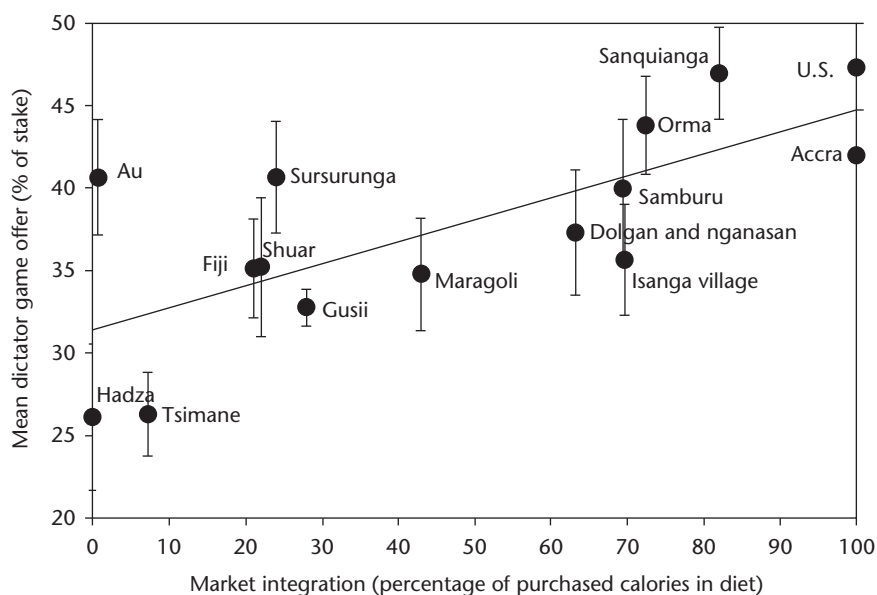


Figure 4 Mean dictator game offers for each population plotted against market integration. Market integration is associated with greater fairness, as measured by an individual's contribution to an anonymous coplayer made in the dictator game across 15 different communities. These findings suggest that new social norms and informal institutions may have emerged in our species to support social interaction in ever-widening socioeconomic spheres with non-kin and strangers. Error bars are bootstrapped standard errors on the population mean. Adapted with permission from Henrich *et al.* (2010). Copyright by The American Association for the Advancement of Science.

Table 1 The difference between adaptive behaviour and adaptations

		Is the behaviour adaptive?	
		Yes	No
Is the behaviour an adaptation?	Yes	Current adaptation	Past adaptation
	No	Exaptation	Dysfunctional byproduct

Source: Reproduced from Laland and Brown (2011) by permission of Oxford University Press.

First, in line with this expanded phenotypic gambit, behavioural ecological models generally assume that the decision-maker has perfect information. Various sorts of models have been developed to deal with the shortcomings of this assumption. Specifically cultural evolutionary theorists (see Henrich and McElreath, 2003) explore mathematically how certain learning or transmission biases may have evolved through the normal processes of natural selection to reduce the costs of arriving at a locally adaptive optimum. In certain circumstances a naïve individual does better to imitate the behaviour of successful individuals in his or her group, or simply do what everyone else is doing rather than experiment with all the perhaps costly strategic alternatives. With such evolved learning biases in place, there arises the possibility for traits to spread that are not adaptive in the strict sense of enhancing individual fitness. Though the extent to which cultural traits parasitise human minds is arguably quite limited, cultural evolutionary processes may well account for apparently maladaptive behaviour (Laland and Brown, 2011). Furthermore they can illuminate some of the more complex aspects of human sociality, such as institutions and hyper sociality. The true nature of cognitive mechanisms may contradict the phenotypic gambit, and thus interfere with current predictions derived from behavioural ecological models.

See also: [Cultural Transmission and Evolution](#)

Second, behavioural ecological models often assume perfectly rational processing of and ability to act on this information. But how can anyone be rational in a world where knowledge is limited and expensive, and where time is often pressing? Evolutionary cognitive psychologists are beginning to explore more psychologically plausible ways in which decisions are made in the real world, with a focus on identifying, through simulation, 'fast and frugal heuristics' (Gigerenzer, 2008). In this respect evolutionary psychology has a real contribution to make to behavioural ecology, by drawing attention more closely to the decision-making apparatus and its constraints. The issue of currencies also needs disentangling; for example, dynamic modelling can be used to determine empirically or reverse engineer what currencies humans appear to be maximising in different domains of their lives (Luttbeg *et al.*, 2000). **See also:** [Sociobiology](#), [Evolutionary Psychology and Genetics](#)

A third often less explicit assumption in the logic of a behavioural ecological approach is that subjects are in evolutionary equilibrium – only under this condition could selection fully account for the observable co-variation between behaviour and ecology. In other words, it is

assumed that our ancestors experienced similar environments over a long enough span of time that rules governing optimal behavioural patterns have emerged. In the study of humans this raises the thorny issue of modern environments, specifically whether there has been sufficient continuity between present and past environments, at least with respect to the critical cues stimulating adaptive behavioural responses. Evolutionary psychologists argue that modern selective environments are very different from those in which human adaptations were forged, and hence that contemporary outcomes are often maladaptive victims of adaptive lag (Laland and Brown, 2011). They therefore emphasise heavily the concept of an 'environment of evolutionary adaptedness' which significantly constrains the adaptiveness of behaviour in the present. The HBE approach, by contrast, argues that we can learn more from the present than from hypothetical scenarios of our past because our behaviour is flexible and tracks changes in the environment.

Because of the problem of modern environments (most acute for humans, but not absent from most other species that experience anthropogenic environmental deterioration), HBE must distinguish different ways in which selection pressures affect, or have affected, traits with respect to our current observations (**Table 1**). An adaptation is a trait that has been shaped by a history of natural selection; if the selection pressures that favoured it in the past are still acting it is a current adaptation, but if the selection pressures have changed such that the trait no longer has a selective advantage it is a past adaptation. Alternatively the trait may not have been selected in the past and either has no beneficial effect in the present (dysfunctional byproduct) or provides some new benefit in the novel environmental conditions of today (exaptation); note that an exaptation can be transformed into an adaptation in the future. Viewing the historical process of adaptation more broadly in this way highlights the need for HBE to coordinate its research agendas across a range of other social science disciplines, from experimental psychology to palaeoanthropology (Mesoudi *et al.*, 2006).

Fourth and finally, behavioural ecologists have not yet entirely grappled with how to deal with the history of the traits under study. In conducting comparative study of the function of traits, biologists now standardly use phylogenetically based comparative methods to control statistically for the common origins of correlated traits, to avoid the problem of statistical dependence (or double counting as adaptations events that only happened once). The method has been introduced quite successfully into HBE

(Mace and Jordan, 2011). However, as an appropriate method for conducting comparative analyses it begs many questions as to how cultural traits spread between different groups and persist over time, and the extent to which these patterns reflect adaptive processes.

Many social scientists remain sceptical if not hostile to the evolutionary perspective embodied in HBE. This stems in part from the relativistic and postmodern agenda that has dominated in many fields, from fashionable antiscience negativism, and from an acute awareness of past abuses of Darwinism (Social Darwinism). At the same time it seems HBE has spilled so broadly into various subfields (Borgerhoff Mulder *et al.*, 2009) in a diverse set of disciplines – economics, psychology, political science, philosophy, demography, reproductive biology, law and conservation biology, as well as the allied fields of archaeology and palaeoanthropology – that its profile is growing enormously. Furthermore, while its simplifying assumptions have been key to the development of the useful theoretical models that are revolutionising our understanding of human behaviour, both past and present, its shortcomings are stimulating new developments in parallel fields of cultural evolution theory and evolutionary psychology.

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