



REVIEW

Human evolutionary psychology and animal behaviour

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Homo sapiens is increasingly being studied within the evolutionary (adaptationist, selectionist) framework favoured by animal behaviour researchers. There are various labels for such work, including evolutionary psychology, human behavioural ecology and human sociobiology. Collectively, we call these areas 'human evolutionary psychology' (HEP) because their shared objective is an evolutionary understanding of human information processing and decision making. Sexual selection and sex differences have been especially prominent in recent HEP research, but many other topics have been addressed, including parent–offspring relations, reciprocity and exploitation, foraging strategies and spatial cognition. Many HEP researchers began their scientific careers in animal behaviour, and in many ways, HEP research is scarcely distinguishable from other animal behaviour research. Currently controversial issues in HEP, such as the explanation(s) for observed levels of heritable diversity, the kinds of data needed to test adaptationist hypotheses, and the characterization of a species-typical 'environment of evolutionary adaptedness', are issues in animal behaviour as well. What gives HEP a distinct methodological flavour is that the research animal can talk, an ability that has both advantages and pitfalls for researchers. The proper use of self-reports and other verbal data in HEP might usefully become a subject of future research in its own right.

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In recent years, 'evolutionary psychology' has become prominent in behavioural science (e.g. Barkow et al. 1992; Bock & Cardew 1997; Simpson & Kenrick 1997; Crawford & Krebs 1998; Johnston 1999; Buss 1999; Gaulin & McBurney, in press), and has been successfully popularized in serious trade books (e.g. Wright 1994; Pinker 1997).

Theory and research to which this label is applied are usually concerned centrally or even solely with *Homo sapiens*. Indeed, evolutionary psychology is often defined as evolutionarily informed study of human mental processes. We consider this taxonomic restriction inappropriate for at least four reasons: because the same approach is being fruitfully applied to other species (e.g. Dukas 1998); because there is a long and honourable tradition of cross-species comparison within psychology itself; because erecting subdisciplinary boundaries along species lines hinders the diffusion of the latest evolutionary thinking into the human

sciences; and because even within human evolutionary psychology, much of the best work is conducted by animal behaviourists who treat *H. sapiens* as 'just another animal'. Thus, in this review, we shall refer to efforts to integrate the study of human psychology and behaviour into the Darwinian framework as human evolutionary psychology (HEP).

For present purposes, HEP encompasses work by nonpsychologists, including even those who have deliberately differentiated themselves from 'evolutionary psychology' as 'evolutionary anthropologists', 'human sociobiologists' and 'human behavioural ecologists'. These approaches are all 'evolutionary' by virtue of their adaptationist, selectionist conceptual framework, and they are all 'psychological' to the degree that they focus on how people acquire and evaluate information and how they use that information in behavioural decision making. In this essay, we review some of the controversies within the community of Darwinists studying *H. sapiens*, as well as some of the complications that arise when animal behaviourists attempt to apply their expertise to the study of this particular, peculiar species.

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WHAT'S NEW?

In both popular and scholarly presentations, evolutionary psychology is commonly portrayed as something 'new'. Why should this be so? Darwin's (1872) painstakingly comparative and evolutionary treatise on the expression of the emotions was, after all, one of the first major works of modern psychological science, and influential early students of the human psyche from Francis Galton and William James to J. B. Watson and Edward Thorndike were avid Darwinians. As the 20th century progressed, however, psychological theory and research somehow lost its evolution-mindedness. Why this shift occurred is beyond our scope, but see Cronin (1991), Degler (1991) and Tooby & Cosmides (1992). In any event, although evolutionary psychology is in one sense as old as Darwinism, and although many scientists (including ourselves) might claim to have been doing evolutionary psychology for decades, there is something new afoot. When we began research on the human animal 20 years ago, publication of an 'evolutionary' paper in a mainstream psychology journal would have been a noteworthy event. Today, there are dozens of journals that at least occasionally publish human research citing both classic and contemporary evolutionary theory and testing psychological hypotheses derived therefrom.

Although psychology lost touch with evolutionary biology, it never abandoned the adaptationist programme. Successful psychologists have always been adaptationists for the same reason that successful physiologists and anatomists have always been adaptationists (Mayr 1983): because the objects of their interest are so clearly organized to achieve various ends. Effective psychological scientists partition their subject matter into component processes with putative functions, and even the most mechanistic of proximate causal investigations derives crucial guidance from assumptions about adaptive function (Daly & Wilson 1995).

The inherent adaptationism of psychological science is especially obvious in the study of sensation and perception, where proposed mechanisms and processes are labelled in terms of the information processing problems that they solve: edge detection, sound localization, olfactory discrimination, image stabilization, light-level compensation, face recognition. A satisfactory functional partitioning of 'higher' mental phenomena has been more elusive, but an adaptationist stance remains almost inescapable. Cognitive psychologists aim to describe the processes by which the mind accomplishes such essential tasks as similarity assessment and categorization, the encoding and retrieval of memories, selective attention, and probabilistic inference. Evolution-minded psychologists (e.g. Sherry & Schacter 1987; Gigerenzer & Hug 1992; Pinker 1997) often complain that their colleagues cling to excessively domain-general notions of what these capabilities entail while overlooking distinct adaptive specializations, and debates continue about the degree to which cognitive processes are modularized and domain specific (e.g. Cosmides & Tooby 1994; Hirschfeld & Gelman 1994).

However, it does not appear that any substantive controversy remains about the validity of the proposition that human cognition comprises a multiplicity of information-processing capabilities, executed by a multiplicity of mental 'organs' and/or 'algorithms' with distinct adaptive functions (see e.g. Gazzaniga 1995).

Even social psychologists have been adaptationists, for they too have repeatedly characterized proposed mental processes in terms of putative functions. Exemplary hypotheses about the functions of social cognition have been that it is organized to minimize 'cognitive dissonance', or to maintain some sort of consistency or 'balance' in one's beliefs and attitudes, or to defend self-esteem. Unfortunately, these proposed intrapsychic functions are often arbitrary with respect to the demands imposed by the external world, including other people, and this, we suggest, is why these theories have risen and fallen more like a succession of fashions than like the building blocks of a cumulative science. Arguably, mainstream social psychology has gone in circles, such that work in the 1990s is in no clear sense an advance over that in the 1950s. Meanwhile, behavioural ecologists and sociobiologists have been making real progress in understanding nonhuman social psychology and behaviour, apparently because they have partitioned the subject along the lines of discrete, real-world problem domains (such as mate value assessment, kin recognition, parental investment allocation, and threat and bluff), and this partitioning carves the psyche more nearly at its joints.

Evolutionary psychologists are convinced that the same approach will also work for the human animal, that is, that the principled postulation and testing of adaptationist hypotheses with explicit attention to how adaptations evolve is the remedy that can rescue psychology's functional theorizing from arbitrariness. Psychologists have always been adaptationists, but they have too rarely been sophisticated selectionists. Freud, for example, read Darwin and cited him respectfully, but apparently never grasped the fundamental Darwinian insight that the ultimate criterion of adaptive functional organization is contribution to fitness (Sulloway 1979); if he had, psychology might have been spared the immense distraction of his fantastic and scientifically fruitless theories (see e.g. Daly & Wilson 1990).

What is 'new' about HEP, then, is simply its relentless application to human beings of the same selectionist perspective that has been so successful in the study of animal behaviour.

IS HEP THE ORDINARY PURSUIT OF ANIMAL BEHAVIOUR RESEARCH WITH A SINGULAR STUDY ANIMAL?

Many prominent contributors to the development of HEP came to the subject from backgrounds in nonhuman animal behaviour, ecology, and evolutionary biology. Such founders of human ethology as Nicholas Blurton Jones, Irenäus Eibl-Eibesfeldt, Robert Hinde and Niko Tinbergen published major works on the behaviour of other vertebrates before turning to the human animal. In the 1970s, entomologist Richard Alexander was an

important instigator of anthropological fieldwork within an adaptationist, selectionist framework, while Harvard animal behaviourists Irvan DeVore, Robert Trivers and Edward O. Wilson inspired a number of Ph.D. students who went on to publish research on both human beings and other animals. Donald Symons, the author of an influential (1979) book on *The Evolution of Human Sexuality*, wrote an earlier monograph on rhesus monkey play, and HEP's two main journals, *Ethology and Sociobiology* (now *Evolution and Human Behavior*) and *Human Nature*, were both founded by scientists (Michael McGuire and Jane Lancaster, respectively) whose research has mainly been on nonhuman primate behaviour. Dozens of other recent contributors to HEP have published on the behaviour of other species, too, usually continuing their nonhuman research in parallel with their human work and often focusing on more or less the same issues in both.

So is HEP just the ordinary pursuit of animal behaviour research, with one self-important primate as the study animal? In many research programmes, that seems to be the case. In recent work on sexual selection and sex differences, for example, researchers (most of whom embrace the evolutionary psychology label) have taken current concepts from theoretical biology and from studies of other animals, and have applied them without essential modification to the study of *H. sapiens*. Many workers have investigated sex differences in polygamous inclinations, sexual jealousy, intrasexual competition, and mate choice criteria from this perspective (e.g. Daly et al. 1982; Wilson & Daly 1985; Buss 1989, 1994; Ellis & Symons 1990; Buss et al. 1992; Kenrick & Keefe 1992; Buss & Schmidt 1993; Singh 1993; Bailey et al. 1994; Symons 1995; Townsend et al. 1995; Herz & Cahill 1997; Miller 1998; Wiederman & Dubois 1998). More specific examples of taking an approach or issue that has been developed in nonhuman sexual selection research and applying it to the human case include explorations of sex differences in spatial information processing in relation to sexually selected ranging behaviour (Gaulin & Hoffman 1988); application of the 'polygyny threshold' model to human marriage transactions (Borgerhoff Mulder 1990); investigation of whether shared MHC alleles have the same effects on sexual attraction in humans that they have in mice (Wedekind et al. 1995); efforts to elucidate the prevalence and consequences of facultative polyandry, extrapair paternity and sperm competition (Baker & Bellis 1989, 1995; Thornhill et al. 1995; Scheib 1997); and a spate of recent work on fluctuating asymmetry as an indicator of 'developmental stability' and phenotypic quality, especially but not solely with reference to the problem of assessing whether women's mate choice psychology exhibits adaptation for gaining 'good genes' benefits independent of material benefits (Thornhill & Gangestad 1994; Manning 1995; Thornhill et al. 1995; Gangestad & Thornhill 1997; Furlow et al. 1998).

Sexual selection has not (quite) been the sole pre-occupation of HEP, and work on other topics has similarly been conducted in close interplay with theory and research in animal behaviour. One example is our

research on violence against children (Daly & Wilson 1988, 1995, 1996), in which risk factors have been predicted from a general theory of evolved facultative variations in parental solicitude. Another is Orians & Heerwagen's (1992) approach to environmental aesthetics as a reflection of psychological adaptations for habitat selection. Meanwhile, a number of anthropologists, despite distinguishing themselves from evolutionary psychology as 'human behavioural ecologists', have been engaged in a similar venture in that they treat people as they would other animals, testing standard optimal foraging theories in traditional societies by painstaking behavioural observation (e.g. Smith 1983, 1991; Hill et al. 1987; Winterhalder 1987). A topic that has attracted interest from both psychologists and anthropologists has been the possible applicability to the human case of some variant of Trivers & Willard's (1973) model of condition-dependent parental preference for sons versus daughters (Dickemann 1979; Voland 1984; Smith et al. 1987; Cronk 1991; Gaulin & Robbins 1991). Even efforts to understand such peculiarly human phenomena as language, artistic production and appreciation, humour and governance routinely invoke the concepts of sexual selection, evolutionary game theory, kin selection, Zahavian handicaps, and other theoretical staples of contemporary animal behaviour research (e.g. Alexander 1986, 1987, 1989; Carroll 1995; Sperber 1996; Constable 1997; Pinker 1997; Miller 1998).

HEP is also an integral part of ordinary animal behaviour science in that its controversies are often matters of concern not only for students of human behaviour but for students of other taxa as well. For example, there has been debate in HEP about the appropriate interpretation of the remarkable levels of heritable diversity in psychological measures and in behaviour (Gangestad 1997). Is this diversity functionless a mere by-product of relaxed selection or the expression of formerly neutral variants in evolutionarily novel environments or frequency-dependent pathogen pressure, as argued by Tooby & Cosmides (1990a)? Or might it instead reflect a substantial prevalence of adaptive polymorphisms, as argued by Wilson (1994)? This is obviously an issue of broad relevance in animal behaviour, rather than one of peculiar relevance to human personality.

Another controversial issue in both HEP and animal behaviour concerns how far the metaphor of evolved psyches as 'strategists' can appropriately be pushed. If we characterize some plant's 'reproductive strategy' by considering the adaptive significance of the ways in which particular cues control germination, growth and dormancy, how its flowering phenology is adapted to the behaviour of its pollinators, and so forth, no one is misled by the language of strategy into imagining that the plant has intentions, much less that those intentions include the maximization of Darwinian fitness. With animals, however, it is more tempting to slip from claims about what the organism is 'designed' to achieve into claims about what it is 'trying' to achieve, and this slip seems to be especially tempting in studies of the human animal, perhaps because people undoubtedly can and do strategize in a more literal sense.

The question of how adaptive functions are related to human goals is at the heart of a wide-ranging and often confusing debate between relatively cognitivist ('evolutionary psychologist') and relatively behaviourist ('human behavioural ecologist') practitioners of HEP. The latter approach got rolling in the 1970s and 1980s, as evolutionary anthropologists tried to test 'the Darwinian hypothesis' that various aspects of people's behavioural preferences have positive reproductive consequences. Controversy was joined when [Symons \(1989\)](#) insisted that measuring reproductive attainment is not the test of a Darwinian approach. If showing that chiefs out-reproduce commoners in some particular society, for example, is portrayed as a demonstration of the relevance of Darwinism to human affairs, would showing that the poor out-reproduce the rich in another society constitute a counterdemonstration? Surely not! In this critique and subsequent elaborations ([Symons 1990, 1992](#); [Tooby & Cosmides 1990b](#)), the more behaviourist researchers were accused of treating inclusive fitness as a motive or objective rather than as the historical arbiter of the selective retention of attributes, and thus of imagining that evolution imparts a magic ability to find the course of action that maximizes inclusive fitness even in the face of evolutionarily unforeseen challenges.

The issue here is largely the old problem of how to integrate 'proximate' and 'ultimate' (or, in the terminology of classical ethology, 'causal' and 'functional') explanations, and this problem persists in animal behaviour, too. A recent exchange in this journal, for example, concerned the links between paternity and paternal care in male songbirds ([Wagner et al. 1996, 1998](#); [Kempnaers & Sheldon 1997, 1998](#); [Lifjeld et al. 1998](#)). Like the debates within HEP, this exchange dealt with the substantive issues of what sort of facultative responsiveness might reasonably be expected to evolve, whether correlations in the absence of experimentation could elucidate causal links, and whether having measures of the actual fitness consequences of behaviour is essential for testing adaptationist hypotheses, and as in the HEP debates, the controversy appears to be at least partly a result of lapses in distinguishing clearly between the role of paternity probability as an ancestral selective force and the proximate causal effects of paternity cues. Also reminiscent of the debates within HEP is the confusion engendered by mentalistic language that implies particular psychological entities and processes that probably do not exist. [Lifjeld et al. \(1998, page 236\)](#) maintain, for example, that 'It is essential that the experiment is carried out in a way that makes the care-giving male aware [sic] that his paternity has been affected', and [Kempnaers & Sheldon's \(1998, page 244\)](#) reply invokes 'certainty of paternity' and 'perceived predation risk' as the proximate causal representations of 'actual genetic parentage' and 'actual predation risk'. It is indeed likely that avian psyches possess functional organization for dealing with these adaptive problems, but that is no reason to suppose that 'certainty of paternity' and 'perceived predation risk' are even functionally equivalent to specific parameters that bird brains actually compute, and even if terms like 'aware' and 'perceived' were never intended to be taken literally, they

seem to us to detract from the elucidation of the actual adaptations controlling the modulation of paternal effort.

If this sort of loosely metaphorical, mentalistic way of discussing 'reproductive strategies' is problematic in animal behaviour, it is that much more so in HEP.

OLD ADAPTATIONS IN NEW ENVIRONMENTS?

Whether one is observing behaviour in an environment sufficiently like that in which the study organism's adaptations evolved is a perennial concern in animal behaviour. Evolved attributes are adapted to the regularities of the past, and their functionality may not be evident in evolutionarily unforeseen settings. In the human case, technological and other changes have been so rapid and pervasive that a 'natural' environment may be unattainable or even unknowable. This issue of the nature and importance of the 'Environment of Evolutionary Adaptedness' (the EEA) has engendered a rather acrimonious and muddled controversy in HEP ([Crawford 1998](#)).

[Tooby & Cosmides \(1990b, pp. 386–387\)](#) stress that the EEA concept does not refer to a single 'place or a habitat, or even a time period. Rather, it is a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and their fitness-consequences'. The point is important, because dissatisfaction with the EEA concept has mostly derived from its equation with a stereotyped Pleistocene savannah. It is surely not controversial that a world with abundant refined sugar, effective oral contraceptives, telephones, novel chemical pollutants, televised violence, personal computers, internet pornography and exogenous opiates must be importantly different from that to which an evolved human nature is adapted, and the idea that mismatches between modern environments and the EEA compromise the effectiveness of human adaptations is one of the cornerstones of 'Darwinian medicine' (e.g. [Williams & Nesse 1991](#); [Eaton et al. 1994](#); [Trevathan et al. 1997](#)). Nevertheless, several evolution-minded anthropologists have been dismissive of arguments that invoke the EEA. [Foley \(1996\)](#) concludes that the EEA concept may once have been useful but is now obsolete, and [Hrdy \(1997, page 34\)](#), in questioning the rationale for expecting men to be attracted to younger rather than older women, heaps scorn on 'an evolutionary psychologist focused on specifically human mental adaptations acquired in some imaginary point in the Pleistocene (the fabled Environment of Evolutionary Adaptedness)'.

Because many of those most hostile to the EEA concept have used it in their own theorizing and research, we suspect that their dissatisfaction is really about something else. [Hrdy's](#) choice of words suggests some annoyance with popular titles like *The Palaeolithic Prescription* ([Eaton et al. 1988](#)) and *The Stone Age Present* ([Allman 1994](#)), but a possibly more important source of antipathy has been the evolutionary psychology/human behavioural ecology debate mentioned above. One component of this debate was a claim by evolutionary psychologists that human behavioural ecologists had been insufficiently concerned

with differences between the modern world and the EEA, such as contraceptive technology, which might have destroyed any association between reproductive success differentials and the proper functioning of psychological adaptations. Defenders of the more behaviouristic approach (some of whom had indeed at least occasionally maintained that demonstrable fitness consequences provide the acid test of a Darwinian hypothesis) counter-attacked, caricaturing the critique as a claim that modern behaviour is ubiquitously maladaptive, and invocations of the EEA as undisciplined speculation about an unknowable past, based on false presumptions both that the ecological and social variability among hunter-gatherer societies is negligible and that human evolution ceased abruptly with the invention of agriculture (Turke 1990; Irons 1998). An irony is that those who deride the EEA concept include researchers who have taken the trouble to study people in nonstate, face-to-face societies, presumably believing that such studies can afford important insights into human nature that could not be attained by studying the citizens of modern mass society.

These disputes often sound as if they are relevant only to the human animal, but they are not. As Thornhill (1997) notes, the idea that measuring fitness consequences (current adaptiveness) provides the best test of adaptationist hypotheses has been advocated by Wade (1987) and by Reeve & Sherman (1993) for more or less the same reasons that it appeals to 'human behavioural ecologists', whereas Thornhill (1990), Williams (1992), and others have taken the opposite tack for more or less the same reasons as have the 'evolutionary psychologists'. Although the term EEA occurs mainly in discussions of human evolution, the concept must apply to any animal. Roitberg et al. (1993) justify their use of barometric pressure as a life expectancy cue for an ovipositing wasp, for example, in terms of what might be called claims about the wasp's EEA. This sort of argument is ubiquitous and essential in studies of captive animals, and the issue arises in field studies as well. When Dunn et al. (1994) found surprisingly high levels of extrapair paternity in tree swallows, *Tachycineta bicolor*, for example, an obvious question was whether this might be an artefact of evolutionarily novel nestbox aggregation, and further testing in the tree swallow EEA (natural nesting cavities) was undertaken (Barber et al. 1996).

It is thus a further irony that it should be self-styled 'behavioural ecologists' who deride the EEA concept as a misconception of the 'evolutionary psychologists', and that Kacelnik & Krebs (1997, page 28) should have felt it necessary to caution them that 'a mechanism evolved under some circumstances may generate inappropriate behavior in others. While attacking small moving objects is an adaptation for insect-eating trout, this mechanism evolved before the proliferation of fly fishing, and there is no reason to believe that present-day trout respond to these stimuli with the readiness that maximizes their fitness. ... The system formed by an organism and its habitat is not in constant equilibrium. We would not understand trout behavior if we thought only about fitness maximization in present circumstances' and that 'Today's humans, like today's trout, use behavioral

mechanisms to follow stimuli that sometimes are just but lures.'

The issue is not simply rhetorical. Interpretive pitfalls await those who disregard the possibility of mismatch between contemporary environments and the EEA. An example comes from recent research on human facial attractiveness and health. Kalick et al. (1998) made ingenious use of a longitudinal health study begun in the 1920s to assess whether facial attractiveness at 17–18 years of age might be related to prior health status and/or predictive of future health status. They could find no such correlations. Moreover, when the contemporary judges that provided Kalick et al. with their attractiveness ratings were asked to guess health status itself from the photographs, they were 'blinded by beauty': their estimates of health status were highly correlated with their attractiveness ratings, and their accuracy in estimating health status was actually better when the effects of attractiveness were statistically removed.

The neglect of EEA considerations arises in the interpretation. Using Cronin's (1991) terminology, Kalick et al. suggest that their results imply that facial attractiveness is not a 'good sense' cue of genetic quality, and must therefore be an arbitrary 'good taste' (Fisherian) cue instead. Furthermore, in light of their null results, Kalick et al. reinterpret Gangestad & Buss's (1993) cross-cultural demonstration that the emphasis given to attractiveness as a mate selection criterion is higher where pathogen pressure is most severe, as indicative of mistaken attributions of good health on the basis of attractiveness in a context where there is a strong, rational interest in the health of possible mates. Kalick et al. do note the possibility that attractiveness was formerly a cue to health, but only with respect to the idea that this enabled the Fisherian process to get underway in some distant ancestor. What they do not appear to recognize is that the ancestral information value of attractiveness cues might have been obscured by modern medicine, good nutrition, or other aspects of life in 20th-century, urban California. (Another unmentioned possibility is that still photographs convey a limited and biased subset of the relevant information, in which grooming and cosmetic manipulations might be sufficient to obscure health status cues and affect attractiveness ratings to a greater degree than they could with less impoverished stimuli.) Thus, although Kalick et al.'s results are certainly interesting and perhaps even challenging to evolutionary psychologists, they fall far short of disproving the hypothesis that the determinants of facial attractiveness acquired their appeal during human evolution because of what they indicated about health status in the EEA.

The general issue is how the peculiarities of modern human environments affect the performance of human adaptations. There is no question that adaptations often misfire in the sense that they fail to promote the actors' fitness. A nice example is Pérusse's (1993) demonstration that whereas high-status men in modern Québec continue to attain more sexual access to women of reproductive age than their lower-status counterparts, this no longer translates into a reproductive advantage. More subtle examples may involve the miscalibration of

inferred parameters of one's social milieu. Kenrick et al. (1989, 1994) found that exposure to a series of photographic portrayals of physically attractive members of the opposite sex induced men, but not women, to devalue their current partners, while a similar effect was induced in women, but not men, by exposure to portrayals of socially dominant members of the opposite sex. The measures in these studies were self-reports of satisfaction with one's current partner, and one may of course question their validity, as we discuss below. Such findings cannot prove that the statistical incidence of exposure to attractive members of the opposite sex really affects the likelihood of mate abandonment, let alone that artificial media portrayals affect this likelihood in the same way as 'real' social experience, but the effect of such portrayals on expressed satisfaction is certainly intriguing and warrants further investigation. In a different domain, if televised violence is really a causal antecedent of youth violence, as many believe, the effects may be mediated by inference processes that normally function to adjust discounting of the future, recklessness, and one's own readiness to use violence to levels appropriate to the prevailing social universe (Wilson & Daly 1997). These are important practical issues and their study could surely profit from the infusion of evolutionists' insights.

THE GARRULOUS ANIMAL

Although *H. sapiens* is increasingly being studied within the conceptual framework applied to other creatures, and although the controversies in HEP echo similar debates in animal behaviour, there remains a distinct methodological flavour to human research, primarily because people talk. Human linguistic ability greatly facilitates the collection of information on everything from matrilineal kinship links, marital and sexual histories, and the bride prices paid for women of different reproductive value, to desires, preferences, attentional priorities, beliefs and grievances. Unfortunately, articulateness of the human animal is a double-edged sword. It has made possible the investigation of questions that one can scarcely imagine how to address in other animals, but it has also tempted researchers down a variety of garden paths.

One obvious problem with relying on human utterances as a primary data source is that interviewees lie. Chagnon (1983), for example, recounts with admirable (and hilarious) candour how he wasted 5 months transcribing Yanomamö obscenities that were solemnly conveyed to him as genealogical information. Some ethnographers never do catch on; the most famous case is that of Margaret Mead, whose distinguished anthropological career was built largely upon her credulous acceptance of Samoan schoolgirls' tall tales (Freeman 1989). Such gullibility may be especially problematic for researchers operating in unfamiliar social settings, but it would be foolish to assume that sharing a culture with one's interviewees is a guarantee against being duped.

More subtle than simple mendacity is the fact that memory is unreliable and its failings are not simply a matter of random information loss or distortion, but exhibit systematic biases (e.g. Ross 1989; Weingardt

et al. 1995). Moreover, and perhaps most importantly, even cooperative interviewees can access and provide testimony about only a small part of the workings of their minds, indeed a smaller part than either they or the scientist questioning them may imagine (Nisbett & Wilson 1977).

At least partly because of skepticism about the validity of self-report data, human ethology initially developed as the behavioural science that approaches the study of human behaviour as if there were no such thing as language. Direct behavioural observation, using scan samples and focal follows, is still the staple methodology in 'human behavioural ecology', an approach that is sometimes championed as addressing what people 'really do' rather than what they 'merely say' (e.g. Cronk 1995). However, although concerns about the validity of self-report data are often well founded, as we shall discuss shortly, what people say is an important part of what they do.

Utterances are consequential acts that warrant investigation within the same adaptationist framework that illuminates other behaviour, and some of the most interesting recent work in HEP has indeed focused on what people say. Examples include Chagnon's (1988) analysis of self-interested manipulations of genealogical information in social discourse and modes of address among the Yanomamö; Buss & Dedden's (1990) analysis of the different ways in which women and men derogate same-sex competitors; Dunbar et al.'s (1997) content analyses of casual gossip; and Salmon's (1998) experimental demonstration that the metaphorical use of kinship terminology has persuasive impact on firstborns and lastborns, who also exhibit other signs of a strongly familial social orientation, but has no such impact on middleborns, whose strongest social ties tend to be reciprocal relationships with nonrelatives. In these and other studies, what people say has been treated as social behaviour in its own right, perhaps representing sincerely informative cooperative acts in some cases and more deceptive acts of disinformation, persuasion and impression management in others. The conceptual framework of these studies is therefore much like the contemporary adaptationist approach to nonhuman communication (e.g. Bradbury & Vehrencamp 1998), notwithstanding the much richer information content of human utterances.

Where reliance on verbal data becomes problematic is when research subjects are, in effect, deputized as data collectors, such that the researcher treats the subjects' recollections as a behavioural record of more or less the same evidentiary status as direct observation. There are substantial bodies of social science research in which the acceptance of interviewees' testimony at face value provides the sole basis for publicized, policy-relevant, empirical claims that are almost certainly false. One noteworthy example was the shocking 'discovery' that husband beating is a hidden social problem of comparable magnitude and severity to the more visible wife beating (Steinmetz & Lucca 1988; Straus & Gelles 1990), a revelation based on questionnaire and interview methods that have been shown to be woefully lacking in reliability and validity (Dobash et al. 1992). However, this example

is not drawn from HEP, and in general, we think that unduly credulous acceptance of self-report data has been a greater problem in some other areas of psychology and the social sciences than in HEP. Some protection against such gullibility perhaps derives from evolutionists' long-standing interests in both self-deception (Lockard & Paulhus 1988) and deceptive self-presentation (e.g. Alexander 1987). Nevertheless, HEP practitioners, like other social scientists, are potentially vulnerable to the siren song of abundant verbal data.

Try asking a random sample of married men what they do when their wives flirt with other men at parties. We predict that not one will reply 'I upregulate the number of sperm in my next ejaculate'. If men really respond in this way, as they may do (Baker & Bellis 1995), then they are unaware of it. You might as well have asked them how much luteinizing hormone their pituitaries secreted yesterday.

Some other kinds of questioning seem intuitively to be less problematic. Most readers of the literature on physical attractiveness, for example, are probably willing to take forced-choice preference tests at face value. If subject X says she finds face A better-looking than face B, then that's her opinion, and that's that. But if we were to ask her whether her ratings were affected by pupillary dilation or nasal symmetry or the length of the chin, we would be naive to assume that she is capable of answering veridically, even if she thinks she can. There is substantial evidence that people lack the introspective access to their own decision processes that such questions require, even when they answer with confidence (Nisbett & Wilson 1977).

Motivation to exaggerate or otherwise deceive may compromise the validity of some kinds of responses, such as the recounting of sexual experiences, whereas for others, such as ranking the criteria underlying a preference, the threat to validity may be more a matter of limited self-knowledge. This distinction begins to break down, however, when we consider that one's self may be among those deceived, as in the case of self-serving biases in one's memory of social interactions past. We are not aware that anyone has undertaken a critical analysis of the reasons why researchers trust certain kinds of self-report data while questioning others, but it seems clear that there is no broad consensus on these issues. Empirical study of researchers' intuitions and prejudices in these matters could be worthwhile, especially if it incorporated tests of their validity.

Asking people how they and others behave in certain situations can be a sensible first step in research. Such 'act nominations' have been used to generate lists of 'tactics' that are then presented to further groups of subjects for affirmation of use by self and others, and for judgments of effectiveness (e.g. Buss 1994; Buss & Shackelford 1997). On their own, such methods are fundamentally dependent on hearsay and possibly biased introspections and observations, raising the concern that one may be studying scripts and stereotypes rather than actual behaviour. Such concerns can often be addressed by the collection of supplementary data of other sorts. Buss et al. (1992), for example, asked women and men which of two

brief infidelity scenarios would be more distressing and found predictable sex differences, but what made their study persuasive was that several physiological measures told the same story. In general, self-report is most convincing when it is complemented by other, less obtrusive and/or less dissimulable measures (e.g. Kenrick & Keefe 1992; Symons et al. 1997).

Questions that require subjects to introspect more deeply, rather than simply to recall actual behaviour or state their preferences, may yield data subject to rival interpretations. Buss (1989) found highly consistent sex differences in how questionnaire respondents from many nations ranked the importance of a given list of mate choice criteria, for example, but although the cross-national consistency of the rankings is certainly interesting, it does not prove that the stated criteria are those by which members of the opposite sex were really evaluated. As Walter (1997) has argued, an equally evolution-minded interpretation of these sex differences in questionnaire responses might attribute them to cross-culturally general sex differences in self-presentation rather than as veridical reflections of sex differences in mate choice criteria. (We should note, however, that complementary data collected by other methods reinforce Buss's conclusion that women and men really do prioritize different criteria in rating the opposite sex; Symons 1995.)

It would be wrong to solve the problems inherent in self-report data by avoiding their use altogether. Verbal reports, including retrospective behavioural data, are too valuable to warrant such a drastic remedy. In practice, even those human behavioural ecologists who are highly skeptical of the validity of questionnaire data, and who have invested hundreds of hours in behavioural scan sampling, almost always supplement their observations with information provided verbally. Analyses that require data on such diverse matters as genealogy, marital and reproductive careers, and variations in material wealth invariably depend on hearsay rather than observation for at least some of their crucial measures. The researcher's confidence in the validity of such data can often be enhanced by cross-checking with multiple informants, and of course mismatches in the information provided by people with distinct interests can be interesting in their own right (e.g. Chagnon 1988; Dobash et al., *in press*).

The matches and mismatches between subjects' articulated preference criteria and the actual determinants of their preferences are amenable to experimental research, as Nisbett & Wilson (1977) have elegantly demonstrated with various sorts of consumer and other choices. This sort of investigation would be a salutary addition to research in HEP. This is not to say, however, that the field has relied excessively on the assumption that people can describe their own evaluative and decision processes. In many cases, theory has directed research attention in HEP to preference and choice criteria of which subjects are quite unaware, such as shared MHC alleles (Wedekind et al. 1995), waist-to-hip ratio (Singh 1993), and certain facial proportions (Grammer & Thornhill 1994; Jones 1996; Johnston 1999).

CONCLUSION

The human animal is assuredly unique. So, of course, is any species, but ours has seemed so different from other animals that the proposition that the social sciences are branches of biology is widely viewed as radical, and even offensive. Most efforts to exempt human beings from the Darwinian world view invoke our species' unparalleled capacity for culture. This is a topic that we cannot begin to address in this brief essay, except to note that evolutionists are heavily engaged in efforts to understand human cultural diversity and culture change (Alexander 1974; Boyd & Richerson 1985; Barkow 1989; Durham 1991; Tooby & Cosmides 1992; Sperber 1996; Flinn 1997; Henrich & Boyd 1998). However, efforts in this area are apparently not so beholden to the animal behaviour research tradition as those we have discussed, despite the interests of some animal behaviourists in social learning and its role in generating and maintaining between-group differences (Galef 1992).

We must also note that there are many productive evolutionary psychologists and anthropologists with no background in nonhuman animal studies, and that there are valuable research programmes in this field that are in no sense derived from animal behaviour studies. Nevertheless, contemporary HEP is very much a child of the science of animal behaviour. Without the contributions of animal behaviourists who took up the study of *Homo sapiens*, HEP would scarcely be recognizable and might not exist at all. Further progress in HEP will undoubtedly continue to be affected by developments in animal behaviour research.

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