Controversies in the evolutionary social sciences: a guide for the perplexed

Eric A. Smith, Monique Borgerhoff Mulder and Kim Hill

It is 25 years since modern evolutionary ideas were first applied extensively to human behavior, jump-starting a field of study once known as 'sociobiology'. Over the years, distinct styles of evolutionary analysis have emerged within the social sciences. Although there is considerable complementarity between approaches that emphasize the study of psychological mechanisms and those that focus on adaptive fit to environments, there are also substantial theoretical and methodological differences. These differences have generated a recurrent debate that is now exacerbated by growing popular media attention to evolutionary human behavioral studies. Here, we provide a guide to current controversies surrounding evolutionary studies of human social behavior, emphasizing theoretical and methodological issues. We conclude that a greater use of formal models, measures of current fitness costs and benefits, and attention to adaptive tradeoffs, will enhance the power and reliability of evolutionary analyses of human social behavior.

Eric A. Smith*
Dept of Anthropology,
University of Washington,
Seattle, WA 98195, USA.
*e-mail: easmith@
u.washington.edu

**Monique Borgerhoff
Mulder**
Dept of Anthropology,
University of California at
Davis, Davis, CA 95616,
USA.

Kim Hill
Dept of Anthropology,
University of New
Mexico, Albuquerque,
NM 87313, USA.

Evolutionary social science is flourishing. Beginning with the innovative syntheses of the 1970s (Refs 1–4), analyses based on evolutionary logic have emerged across all the traditional social science disciplines, including anthropology, economics, environmental studies and political science, as well as in literature, law and medicine. The topics analyzed range from motherhood to warfare, sexuality to language, and religion to rape. The contributors to this literature are equally diverse, including ethologists, entomologists, linguists, lawyers, paleoecologists, philosophers and experimental psychologists. Despite the range of topics and fields represented, these contributions all draw on the fundamental theoretical insights of Charnov, Hamilton, Maynard Smith, Trivers and Williams, with the logic of adaptation by natural selection providing a framework for theoretically unifying the human sciences to a degree not seen in over a century.

However, beneath this apparent unity lie serious theoretical and methodological disagreements. Given the diverse backgrounds of the practitioners, it is hardly surprising that evolutionary social science contains several distinct styles of analysis, reflecting the methodological and conceptual habits of the parent disciplines. Although sharing a commitment to formulating and testing adaptive explanations of human behavior, these various approaches have produced rather different bodies of research and sometimes competing perspectives on human behavior. This is clearly exemplified by the two most prominent approaches, evolutionary psychology and human behavioral ecology.

As the name suggests, evolutionary psychology applies evolutionary reasoning to psychological phenomena[5,6]. The goal of evolutionary psychology is to uncover 'the psychological mechanisms that underpin human…behavior…and the selective forces that shaped those mechanisms'[7]. Evolutionary psychologists generally posit that the behavior of any species (including humans) is produced by specialized cognitive 'modules' that evolved in response to specific adaptive problems in past selective environments[8]. They investigate these cognitive mechanisms primarily with data gathered through laboratory studies (reflecting the methodological traditions of academic psychology) and surveys or public databases, using standard statistical methods and experimental controls. For example, the hypothesis that ancestral humans evolved a specialized 'cheater-detection module' to facilitate delayed reciprocity has been tested by analyzing responses to logic tests[9]. Typically, the hypotheses examined by evolutionary psychologists are generated through informal inference rather than through mathematical deduction.

Human behavioral ecology applies the theoretical perspective of animal behavioral ecology[10] to human populations, examining the degree to which behavior is adaptively adjusted to environmental (including social) conditions, emphasizing conditional strategies of the form 'in situation X, maximize fitness payoffs by doing α; in situation Y, do β'. For example, one might see if birth rates vary according to ecological circumstances in a manner that maximizes reproductive success (Box 1). Research in human behavioral ecology emphasizes naturalistic field tests of hypotheses deduced from optimality and game-theory models. Typically, it pays greater attention to the relationship between environmental constraints and behavioral strategies than to determining precisely how individuals attain those strategies. From its beginning in the mid-1970s, human behavioral ecology has emphasized foraging and reproductive strategies[11,12] and the field has now produced several hundred scholarly publications[13].

What is the fuss about?

Initially, scholars committed to an evolutionary approach to human behavior sought common cause in the face of widespread hostility to evolutionary analyses of human behavior during the sociobiology debate of the 1970s. But in 1987, Donald Symons (a primatologist turned student of human sexuality) published an essay[14] entitled 'If we're all Darwinians, what's the fuss about?'. In this essay, Symons

Box 1. How to maximize your descendants

Several studies of traditional human societies have investigated whether parents produce an optimal number of offspring, following the logic of Lack[a] and Smith and Fretwell[b]. Blurton Jones[c] showed that among southern African !Kung San foragers, a lengthy 48-month interval between births was the modal pattern, and reduced child mortality enough to maximize the number of surviving offspring that the women raised in their lifetimes. By contrast, among the Ache of Paraguay, there is no evidence that infant mortality is associated with either the number of siblings or the length of the birth interval preceding the child's birth, a finding that might be due to rapid growth in the Ache population during the pre-contact period that was sampled demographically[d]. In modern, low-fertility populations, human behavioral ecologists have often posited that small family sizes are optimal with respect to fitness, given the extraordinary high costs of raising offspring. Data to show that intermediate-sized families are optimal

Fig. I

TRENDS in Ecology & Evolution

with respect to the production of grandchildren have been lacking[e]. However, in an agropastoral Kenyan community that faces severe competition between sons for the land and livestock crucial to a successful reproductive career[f], intermediate-sized families do appear to be optimal with respect to the production of grandchildren, at least for women[g]. As shown in Fig. I, if we subdivide data on Kenyan Kipsigis women according to both surviving offspring per woman and wealth classes (based on their husband's land ownership), the number of grandchildren peaks at intermediate levels ($p < 0.05$). Therefore, this study contributes to the attempts of behavioral ecologists to specify the social and ecological conditions that might favor the adoption of varying (but locally adaptive) levels of fertility.

References

a Lack, D. (1947) The significance of clutch size. *Ibis* 89, 302–352

b Smith, C.C. and Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *Am. Nat.* 108, 499–506

c Blurton Jones, N.G. (1986) Bushman birth spacing: a test for optimal interbirth intervals. *Ethol. Sociobiol.* 7, 91–105

d Hill, K. and Hurtado, A.M. (1996) *Ache Life History: The Ecology and Demography of a Foraging People*, Aldine de Gruyter

e Borgerhoff Mulder, M. (1998) The demographic transition: are we any closer to an evolutionary explanation? *Trends Ecol. Evol.* 13, 266–270

f Borgerhoff Mulder, M. (1998) Brothers and sisters: how sibling interactions affect optimal parental allocations. *Hum. Nat.* 9, 119–162

g Borgerhoff Mulder, M. (2000) Optimizing offspring: the quantity–quality tradeoff in agropastoral Kenyan Kipsigis. *Evol. Hum. Behav.* 21, 391–410
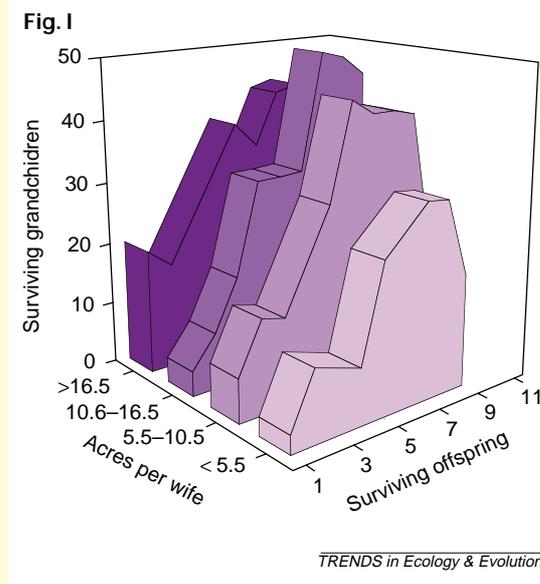
mounted an attack on what he called 'Darwinian anthropology' (actually, classic human sociobiology), and advocated an alternative approach focused on evolved psychological mechanisms. This salvo ignited a debate over the correct way to study human behavioral adaptation, and helped launch evolutionary psychology as a distinct field. Although some recent publications[15–17] have emphasized the complementarity between evolutionary psychology and other approaches, major disagreements remain. Despite appearances, this debate is more than a parochial turf battle involving a narrow set of participants; it should concern anyone interested in (or worried about) the role of evolutionary explanation in human affairs, for several related reasons.

First, evolutionary studies of human behavior are receiving extraordinary attention from the popular media. Every week, there are spirited debates in national newspapers on topics such as the evolution of religion or morality, magazine articles on polyandry or the evolutionary secrets of beauty, and risqué late-night talk shows discussing evolutionary rationales for the sexual indiscretions of politicians. There is a common weakness to these exposés: a tendency to engage in 'just-so' story telling only loosely aligned with evolutionary logic, let alone to rigorous data. Sometimes, it appears that authors are tempted to sacrifice accuracy and intellectual caution for media attention. We suspect that there are few current areas of evolutionary and ecological research where the popular : primary literature ratio is so high, making it imperative to lay out clearly the methodological and conceptual debates and caveats.

Second, most academics are too busy to read primary literature unrelated to their own

specialization, and we are all increasingly relying on popularized syntheses. For this reason, we suspect that the general picture *Trends in Ecology & Evolution* readers have of evolutionary social science is represented by a recently published Perspective by Pigliucci and Kaplan[18]. Referring to a prominent review article by Daly and Wilson[19], Pigliucci and Kaplan suggest that 'a new brand of sociobiology, renamed "evolutionary psychology", seems to be retracing its ancestor's path of mistakes by making wild claims on the genetic basis of human behavior while ignoring the two decades of debate about the adaptationist program'. Daly and Wilson do not make such claims, but those exposed to evolutionary psychology (or other approaches in evolutionary social science) primarily through the popular literature might easily come to this conclusion.

Third, and most importantly, the various styles of evolutionary social science are historically distinct and have developed quite different research traditions. Contrary to the increasingly prevalent belief that evolutionary psychology encompasses the work of all those involved in evolutionary analyses of human behavior, we contend that these research traditions differ in important theoretical and substantive ways[20]. Specifically, these differences involve: (1) the role of formal models and deductive theory; (2) the postulated specificity and rigidity of evolved psychological mechanisms; (3) assumptions regarding the prevalence of adaptive lag and the nature of adaptation to past environments; and (4) the theoretical and methodological relevance of fitness measures to analyses of contemporary behavior. These divergences have several major consequences for analyses of human behavior, as we now hope to show.

'Adaptation executers' or 'fitness maximizers'?
Some researchers suggest that human minds consist of 'mental modules' running 'Darwinian algorithms' that solve discrete social problems such as mate choice, free-rider detection and parental solicitude. From this perspective, organisms (including humans) are 'adaptation executers' that respond to environmental cues in any specific domain (e.g. mate choice) using mental modules evolved for that specific purpose in past environments[8].

By contrast, other researchers are less interested in the structure of the mind than in its behavioral output and, therefore, employ relatively simple analytical models, based on optimality methods[21] or evolutionary game theory[22], to generate predictions concerning behavior. Optimization analysis focuses on tradeoffs, such as fewer offspring for ones of higher quality, or lower food intake for better predator avoidance. Solving such tradeoffs requires some goal or currency that is maximized; in evolutionary studies, this currency is either inclusive fitness (of the focal individual), or some proxy such as nutritional status[23] or offspring survival[24]. Although this

approach makes few explicit assumptions about cognitive architecture, it implies great flexibility (behavioral phenotypes with wide reaction norms, in the parlance of developmental biology) and the ability to behave adaptively in a wide range of environments.

Critics of the fitness-maximization perspective characterize it as a form of naive adaptationism that lacks scientific rigor. They criticize appeals to fitness maximization for confusing proximate motivation with evolutionary mechanism[19] (after all, organisms do not strive to maximize fitness, but rather to obtain food and mates, avoid predators and parasites, and so on). They further argue that adaptations are designed to solve specific adaptive problems, such as pumping blood (hearts) or selecting mates (mate-choice algorithms)[25,26]. Some evolutionary psychologists go so far as to argue that designing organisms to maximize fitness is impossible, tantamount to assuming that individuals have 'a magic ability to find the course of action that maximizes inclusive fitness'[19]. Thus (we have heard it claimed), you can program a robot to sweep a room, or to stamp envelopes, but you cannot program one to maximize fitness. Similarly, the view that evolution will favor a collection of specialized cognitive modules designed to solve various adaptive problems over a general-purpose optimality synthesizer is promoted (in one popular metaphor) by citing the superiority of the multitool Swiss Army knife over an all-purpose pocket knife.

What responses have been made to such arguments? First, the specificity of evolved mechanisms is a matter to be established empirically rather than accepted *a priori*. For example, although adaptive explanations of human polyandry might seem to imply a specific 'polyandry module' evolved in the remote past[7], such practices might arise as an expression of a more generalized ability to vary behavior concerning marriage and property rights in locally adaptive ways[27]. Second, the existence of numerous distinct modules is somewhat at odds with the common conception of evolution proceeding by 'tinkering' with existing evolved traits[28] and co-opting them to solve novel adaptive problems.

Third, the specialized-module framework fails to specify how the different modules might fit together (a fundamental theoretical issue given the tradeoffs that lie at the heart of evolutionary optimization). Unlike a robot designed to excel at sweeping or stamping, natural selection is unlikely to design organisms to maximize outputs of any particular task; rather, selection should favor organisms that optimize these abilities (trade off amounts and efficiencies in each), thus maximizing their chances of surviving and reproducing. If efficient foraging conflicts with efficient mate-guarding and/or efficient childcare, how will specialized mechanisms for each of these domains be designed to interact? Unlike the specialized robot, effective adaptive design requires integrative mechanisms for measuring tradeoffs (which themselves vary in complex and contingent ways), and

adjusting behavior according to the weighted effect of different activities on expected inclusive fitness.

This last point bears on one of the most controversial issues facing evolutionary analyses of human behavior. The image conveyed in some very influential accounts of human behavioral adaptation is of individuals enacting a series of scripts fashioned in our remote evolutionary past that might or might not make sense in the modern world but still constrain us to act in rather stereotyped ways: for example, males selecting mates on the basis of youthfulness, hip : waist ratios, and other invariant cues of fertility and health, and females selecting mates on the basis of status or resources[29]. Two decades of research on the psychological adaptations underlying mating preferences has generated a list of the sexual and parental cues men and women look for in mates, but almost no information on how these cues are contextually weighted, how they interact with one another, and how they are used in the real world of mating markets and biological clocks[30]. By contrast, the optimality approach suggests that because mate acquisition involves tradeoffs with other adaptive domains, a more flexible and socially attuned decision-maker is needed[31]. In effect, the Swiss Army knife needs an intelligent actor who can employ it in an adaptive (fitness-enhancing) manner, selecting the right tool for the job at hand, or even improvising if no 'built-to-order' tool is available.

Recent research on possible interactions between mating, parenting and subsistence is providing some interesting insights into human reproductive behavior. For example, in societies ranging from African hunter–gatherers[32] to urban America[33], care-giving and provisioning by stepfathers is commonplace in many social settings where marital instability is high, and is modulated in ways that suggest that it is designed to attract or maintain mating access to the mother[34,35]. Thus, although males do invest less in stepchildren than in biological offspring, and stepfathers pose a statistically higher source of abuse than biological fathers[36], mating constraints and female choice can significantly moderate these tendencies. Even from a darwinian perspective, stepfathers are not necessarily as uncaring or dangerous as some simplistic popularizations would suggest.

Tradeoffs between parenting and subsistence are also common, and might shape human life histories, patterns of maternal–kin cooperation, and food-sharing in complex ways[24,37–39]. For example, a recent study in a Melanesian community provides evidence that cooperative sea-turtle hunting to provision feasts is a form of costly signaling in which hunters sacrifice foraging efficiency to gain status and, ultimately, reproductive advantage[40,41]. The broader conclusion suggested by these studies and others[42], is that behavioral tradeoffs between different goals are common, and that solutions that maximize fitness given these constraints are likely to evolve.

Adaptive lag and the 'EEA'

The genetic evolution of complex adaptive design is a slow process. From this relatively uncontroversial starting point, some researchers have drawn rather sweeping conclusions: (1) all adaptations are solutions to recurrent adaptive problems in the remote past (which, following Bowlby[43], is often termed the 'environment of evolutionary adaptedness' or EEA); (2) therefore, 'a well-formed description of an adaptation must consist solely of words for things, events, relations, and so forth, that existed in the EEA, which, in the case of human beings, means the Pleistocene world of nomadic foragers'[25]; (3) there is a yawning gulf between the EEA to which our domain-specific mechanisms are adapted, and the dramatically novel present, in which these mechanisms produce 'mismatches' that 'compromise the effectiveness of human adaptations'[19]. In other words, we have 'stone-age minds' faced with modern (evolutionarily novel) conditions; (4) given points (1) and (3), the resultant adaptive lag 'might have destroyed any association between reproductive success differentials and the proper functioning of psychological adaptations'[19]; and (5) hence, it follows that measures of current fitness are 'irrelevant' to determining the adaptive significance of human behavior[25]. Positive correlations of hypothesized adaptations and fitness might well be spurious, whereas negative measures could simply mean that phenotypes that were once fitness enhancing no longer have this effect in novel environments.

These claims have been challenged on several grounds. Paleoanthropologists and others question the validity of the EEA construct (1), or at least its definition as the Pleistocene world of hunter–gatherers, pointing out that the Pleistocene encompassed a highly variable set of environments and hominid social systems[44]. Although some selective factors or constraints are ancient (e.g. the sex differences associated with internal fertilization, gestation and lactation), others were altered a few millennia ago with the rise of agriculture and urbanization, enough time for at least some genetic evolution to have occurred[45,46]. Many researchers emphasize the flexibility of human adaptive mechanisms, and propose that evolved conditional strategies, learning biases and social information transfer[47] will produce adaptive outcomes most of the time, even in relatively novel environments. To the extent that empirical evidence supports this last prediction, we can conclude that only the environmental details are novel, not the fundamental tradeoffs they present, nor the ability to recognize and appropriately react to those tradeoffs.

The idea that there must be a point-by-point match between selective features of the EEA and specific mechanisms guiding adaptive behavior (2) has also been questioned[27]. Because motor vehicles were not part of the EEA, does this mean that the evasive

actions of wary pedestrians fall outside the purview of adaptive analysis? Or did the past existence of falling boulders and charging rhinos select for a cognitive module general enough to minimize the chances of collision with large moving objects, whether they be rhinos or Range Rovers[48]? Or are the relevant evolved mechanisms even more general, having to do with motion detection, aversion to personal injury, and imitative learning? The verbal arguments of EEA proponents that seemed so incisive and revolutionary are compatible with any or all of the above, and hence rather lacking in predictive content.

Controversy over adaptive lag (3) and the relevance of fitness measures (4 and 5) has been extensive[15,16,27,48,49]. Those who attack the use of fitness measures often do so on the basis of assumption or anecdotal evidence. Assertions regarding the maladaptive effects of modern birth control and the demographic transition (reduction in family size with modernization)[19] or the absence of any current fitness-related payoff to contemporary risk-taking behavior such as extreme sports[50], are taken at face value. Empirical evaluation of these widespread assumptions is rare, in part because most researchers who use fitness-based currencies study small indigenous populations rather than urban/industrial ones. But, if the divide between the EEA and environmental novelty lies at the foraging-agriculture boundary, there is a substantial set of studies of subsistence farmers and pastoralists that qualify[13], including a growing number based on historical records from complex, nearly modern contexts[42]. This evidence suggests that any transition to societies where fitness measures of adaptive variation have reduced predictive power is much more recent than the end of the Pleistocene, and involves industrial production, formal education and artificial contraception[51].

Even the most ardent supporters of fitness-calibrated tests of adaptationist hypotheses recognize some limitations: measuring fitness or any of its components (e.g. reproductive success or survivorship) is often difficult, inefficient or otherwise inappropriate. Are there any drawbacks to not using fitness measures? If adaptations are designed to solve specific problems (the heart to pump blood, the beauty-evaluation module to detect youthful and healthy females, and so on), then why not just measure how well they do these things? There are two major objections that can be raised to such proposals.

First, there is the problem posed by adaptive tradeoffs. Although physiological and behavioral phenotypes are indeed specialized to perform specific functions, evolutionary logic suggests that they face significant design constraints reflecting the multiple goals of living organisms. If the heart were designed to be simply an effective blood pump, we would expect it to be larger and beat at a relatively constant speed; however, it is constrained in size and performance because the goal of optimal blood flow is traded off

against other fitness-related goals and other uses of energy. Given these constraints, natural selection has designed the heart to be a 'fitness-maximizing pump' rather than simply a blood pump. This is a crucial distinction that many proponents of domain-specific adaptation fail to grasp.

Second, there are real limitations to generating predictions about adaptive design from scenarios of how selection shaped a given adaptation in the EEA. The literature is replete with assertions that some particular trait, such as male competitiveness or risk-taking[50,52], would have enhanced the fitness of its bearers in ancestral environments, and that is why it occurs now. Such hypotheses might be plausible, but they are also often untestable. Ruling out any contemporary investigation of fitness outcomes produces an analysis based on the least measurable selection pressures, those hypothesized to have occurred in our remote evolutionary history. Although reasonable precautions must be taken with respect to adaptive lag and spurious correlations, even greater pitfalls face those who rely on adaptive story telling while eschewing optimization models and fitness measures.

The rape-as-evolved-adaptation controversy

These and other caveats discussed above provide a useful perspective on a current controversy in evolutionary social science. A recent book by Thornhill and Palmer[53] proposes that rape might be the expression of a domain-specific adaptation that evolved as a male reproductive strategy in the EEA (although leaving open the possibility that rape might simply be a byproduct of 'simultaneous arousal and coercive inclinations'). This book has attracted considerable controversy and sensationalized press coverage but, in our view, its primary scientific weaknesses are the lack of explicit models or fitness measures, and the appeal to hypothetical domain-specific evolved psychological mechanisms.

We suggest that a more effective evaluation of the rape-as-evolved-reproductive-strategy hypothesis requires specification of an evolutionary model, and estimates of the fitness costs and benefits of rape. Ideally, these estimates should be based on quantitative data from several traditional societies (natural-fertility populations of hunter–gatherers or tribal people). As a preliminary exercise (Box 2), we use the most complete data available, from a single group of hunter–gatherers[24], in order to estimate fitness costs and benefits of a single rape by a male aged 25 years (compared to an otherwise identical nonraping male). We assume that most rapes are reported or detected, and that rapists target only reproductive-aged women resident in their own community.

Although our list of parameters and estimates of their values is meant to be heuristic, and is certainly not definitive, we have not knowingly excluded factors that could plausibly alter the balance in favor of the

Box 2. Is rape an evolved reproductive strategy?

The recent book by Thornhill and Palmer[a] on the evolutionary significance of rape has provoked much controversy. To illustrate the advantages of a specifically hypothetico-deductive research strategy over more intuitive approaches, we offer a heuristic but explicit model. Because most costs of committing rape involve death, injury or status reduction, whereas gains are measured in offspring produced, all costs and benefits of a single rape event must be converted into the common currency of reproductive value, scaled to 1 (the reproductive value of a female offspring at birth in a stationary population), to assess the tradeoff involved[b]. Thus, fitness costs are measured in lost reproductive value, and the gains in offspring produced are measured as additions to reproductive value. The following variables define these costs and benefits, illustrated with measurements (variables A, H and I) or estimates (from extensive demographic interviews) based on fieldwork among the Ache Indians of Paraguay[c]:

A – Reproductive value of an average (nonraping) 25-year-old male = 2.4

B – Proportion surviving owing to retaliation by the victim = 0.995

C – Proportion surviving owing to retribution by victim's husband or kin = 0.99

D – Proportion surviving owing to loss of alliances = 0.995

E – Proportional fertility owing to status loss = 0.99

F – Inclusive fitness cost from impact of rapist's behavior on close kin = 0.005

Total cost to rapist, per rape is measured by: $A – ABCDE + F = 0.0762$

H – Probability that a reproductive-aged woman is having ovulatory cycles (given rates of pregnancy and lactational amenorrhea in traditional populations) = 0.15

I – Probability that an ovulating woman will conceive, per rape = 0.07 (2/28)

J – Proportion of fetuses surviving owing to rape-related abortion = 0.9

K – Proportion of infants surviving owing to rape-related infanticide = 0.9

L – Proportion of children surviving owing to rape-related parental neglect = 0.95

M – Proportional adult mating success of child given rape-related status = 0.95

Total expected increment in the rapist's reproductive value, per rape is measured by $HIJKLM = 0.0078$

Thus, given the estimated parameter values, our model predicts that the fitness cost of committing a rape exceeds the benefit by an order of magnitude. Whereas these quantitative results are based on specific parameter values, the qualitative result (costs > benefits) are quite insensitive to these values. The qualitative result holds even if we completely eliminate any single model parameter except I (the probability of impregnation of an ovulating rape victim); and holding other parameter values constant, I would have to exceed 0.695 (nearly five out of seven cases) to produce a net benefit. Based on our experience in small-scale societies, we assume that knowledge of the rape always becomes widespread; but reducing the incidence of

discovery to 50% would still leave predicted rape costs (0.044) much higher than the benefits (0.009). Whereas the payoff to rape might be increased by the rapist avoiding pregnant and lactating women, it would still not be high enough to favor rape; and if selection of victims was similar to that reported in modern societies (where a large fraction of rape victims are pre- and postreproductive women)[a] the likelihood of rape being an evolved adaptation is even lower.

Finally, our model is designed for situations where rapist and victim belong to the same community; rape during raids on enemies might reduce many costs close to zero. But, even if such rape opportunities arose as often as once per year, they would increase a 25-year-old male's expected lifetime reproduction by only 0.4%, making selection for special rape mechanisms in warfare extremely weak relative to other factors that influence male fitness. Rape in large, urban, relatively anonymous settings might also have low costs, but this context is evolutionarily novel and hence irrelevant to the question addressed by our model, the plausibility of Thornhill and Palmer's hypothesis of a specially evolved rape adaptation.

References
a Thornhill, R. and Palmer, C. (2000) *A Natural History of Rape: Biological Bases of Sexual Coercion*, MIT Press
b Charlesworth, B. and Charnov, E.L. (1981) Kin selection in age-structured populations. *J. Theor. Biol.* 88, 103–119
c Hill, K. and Hurtado, A.M. (1996) *Ache Life History: The Ecology and Demography of a Foraging People*, Aldine de Gruyter

evolution of rape. If anything, we have been conservative in estimating the costs of raping; for example, our model assumes no opportunity cost of time and energy expended in the rape (which could be significant if successful rape required extensive planning and time incurred waiting for an appropriate opportunity). Note that none of the effective counter strategies to rape included in our model require rape in order to evolve or be maintained in a population. They might all be favored in any environment where unwanted pregnancies associated with low paternal investment are a common risk and women or their kin have strong disincentives to invest in such children[31], and where individuals who commit acts detrimental to others are punished[54].

The model predicts that, with the estimated parameter values, the total fitness cost of committing

a rape is an order of magnitude higher than the expected benefit. This suggests that only men with an expected reproductive value of ≤1/10 that of an average 25-year-old can benefit from rape. Whether such men are common in a population and how frequently they would have opportunities to rape are crucial to determining whether a specific rape adaptation would be favored by selection. Because the expected payoff from a rape is so low, few, if any, men should be disposed to use rape as a reproductive strategy unless the cost is near zero. Although this conclusion is based on our particular estimates, it is important to stress that it is insensitive to moderate variation in our estimates of each of the variables listed above (Box 2).

The most important contribution of a formal model of evolutionary tradeoffs for any hypothesized

adaptation is that, by specifying the assumed costs and benefits, it clarifies what must be measured to test the adaptive hypothesis. Such models also help generate novel predictions. For example, the model in Box 2 suggests that, if rape were an evolved reproductive strategy, older men would be more likely to rape, because they have less reproductive value to lose from violent retribution or status reduction. These and other hypotheses deducible from a formal model are falsifiable with empirical data, including measures of behavioral impacts on fitness components, something difficult to do within the theoretical and methodological framework employed by Thornhill and Palmer.

Prospects

Many of the issues discussed here have implications for the whole field of behavioral ecology and animal behavior[49]. Mechanism specificity and tradeoffs between different adaptive goals are pertinent to all species, and are receiving increasing attention in behavioral ecology. The issue of adaptive lag might be more pertinent to humans than to other species, although global environmental change is bringing that into question. To the extent that anthropogenic environmental change is intentional, and thus guided by evolved goals, it might often serve human fitness interests – an expectation consistent with the remarkable growth of the human population.

The extensive use in behavioral ecology of formal models to generate testable hypotheses accounts for much of the progress in evolutionary research on animal behavior over the past three decades. Consequently, far from abandoning these methods in the study of humans, we think that their use should be expanded. How to study human decision making from an evolutionary perspective, how well these decisions might track current fitness optima, and the extent to which decisions map onto actual cognitive mechanisms, are all current questions[55], generating some truly innovative research among evolutionary thinkers[56–59]. Our goal in reviewing the debates within evolutionary social science is not to demote the importance of any one approach, such as evolutionary psychology. Indeed, theoretical and methodological plurality becomes increasingly important as the scope of topics falling under evolutionary scrutiny expands.

However, we do want to raise caveats over some developments in a young and provisional science, particularly when these become popularized. Some rather inflammatory claims, based only loosely or speculatively on evolutionary theory, are in danger of diverting even scholarly attention from more careful and sophisticated research. There is a growing danger that careless popularizations, adaptationist story-telling and overly rigid views of human decision-making mechanisms will produce an inevitable backlash against all evolutionary approaches in the social sciences, irrespective of the assumptions and methods employed. Given all the valuable research on human behavioral adaptation from a variety of theoretical and methodological perspectives that has emerged in the past few years, this would be unfortunate.

References

1 Wilson, E.O. (1978) *On Human Nature,* Harvard University Press
2 Dawkins, R. (1976) *The Selfish Gene,* Oxford University Press
3 Alexander, R.D. (1979) *Darwinism and Human Affairs,* University of Washington Press
4 Chagnon, N.A. and Irons, W.G., eds (1979) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective,* Duxbury Press
5 Barkow, J.H. *et al.*, eds (1992) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture,* Oxford University Press
6 Buss, D.M. (1999) *Evolutionary Psychology: The New Science of the Mind,* Allyn and Bacon
7 Symons, D. (1992) On the use and misuse of Darwinism in the study of human behavior. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Barkow, J. *et al.*, eds), pp. 137–159, Oxford University Press
8 Tooby, J. and Cosmides, L. (1990) The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethol. Sociobiol.* 11, 375–424
9 Cosmides, L. and Tooby, J. (1992) Cognitive adaptations for social exchange. In *The Adapted Mind; Evolutionary Psychology and the Generation of Culture* (Barkow, J. *et al.*, eds), pp. 163–228, Oxford University Press
10 Krebs, J.R. and Davies, N.B., eds (1997) *Behavioural Ecology: An Evolutionary Approach* (4th edn), Blackwell

11 Smith, E.A. and Winterhalder, B., eds (1992) *Evolutionary Ecology and Human Behavior*, Aldine de Gruyter
12 Borgerhoff Mulder, M. (1991) Human behavioral ecology: Studies in foraging and reproduction. In *Behavioral Ecology: An Evolutionary Approach* (Krebs, J. and Davies, N., eds), pp. 69–98, Blackwell
13 Winterhalder, B. and Smith, E.A. (2000) Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evol. Anthropol.* 9, 51–72
14 Symons, D. (1987) If we're all Darwinians, what's the fuss about? In *Sociobiology and Psychology: Ideas, Issues and Applications* (Crawford, C. *et al.*, eds), pp. 121–146, Erlbaum
15 Borgerhoff Mulder, M. *et al.* (1997) The place of behavioral ecological anthropology in evolutionary social science. In *Human by Nature: Between Biology and the Social Sciences* (Weingart, P. *et al.*, eds), pp. 253–282, Erlbaum
16 Sherman, P.S. and Reeve, H.K. (1997) Forward and backward: alternative approaches to studying human social evolution. In *Human Nature: A Critical Reader* (Betzig, L.M., ed.), pp. 147–158, Oxford University Press
17 Smith, E.A. (2000) Three styles in the evolutionary study of human behavior. In *Human Behavior and Adaptation: An Anthropological Perspective* (Cronk, L. *et al.*, eds), pp. 25–44, Aldine de Gruyter
18 Pigliucci, M. and Kaplan, J. (2000) The fall and rise of Dr Pangloss: adaptationism and the Spandrels paper 20 years later. *Trends Ecol. Evol.* 15, 66–70

19 Daly, M. and Wilson, M. (1999) Human evolutionary psychology and animal behaviour. *Anim. Behav.* 57, 509–519
20 Smith, E.A. *et al.* (2000) Evolutionary analysis of human behaviour: a commentary on Daly and Wilson. *Anim. Behav.* 60, F1–F6.
21 Parker, G.A. and Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature* 348, 27–33
22 Dugatkin, L.A. and Reeve, H.K., eds (1998) *Game Theory and Animal Behavior*, Oxford University Press
23 Sellen, D.W. (1999) Polygyny and child growth in a traditional pastoral society: the case of the Datoga of Tanzania. *Hum. Nat.* 10, 329–371
24 Hill, K. and Hurtado, A.M. (1996) *Ache Life History: The Ecology and Demography of a Foraging People*, Aldine de Gruyter
25 Symons, D. (1989) A critique of Darwinian anthropology. *Ethol. Sociobiol.* 10, 131–144
26 Tooby, J. and Cosmides, L. (1992) The psychological foundation of culture. In *The Adapted Mind; Evolutionary Psychology and the Generation of Culture* (Barkow, J. *et al.*, eds), pp. 19–136, Oxford University Press
27 Smith, E.A. (1998) Is Tibetan polyandry adaptive? Methodological and metatheoretical analyses. *Hum. Nat.* 9, 225–261
28 Jacob, F. (1977) Evolution and tinkering. *Science* 196, 1161–1166

29 Buss, D.M. (1994) *The Evolution of Desire*, Basic Books

30 Miller, G.F. (1997) Mate choice: from sexual cues to cognitive adaptations. In *Characterizing the Human Psychological Adaptation. CIBA Foundation Symposium 208*, pp. 71–82, John Wiley & Sons

31 Hrdy, S.B. (1999) *Mother Nature: A History of Mothers, Infants, and Natural Selection*, Pantheon Books

32 Marlowe, F. (1999) Male care and mating effort among Hadza foragers. *Behav. Ecol. Sociobiol.* 32, 57–64

33 Anderson, K.G. *et al.* (1999) Paternal care by genetic and step fathers I: reports from Albuquerque men. *Evol. Hum. Behav.* 20, 405–431

34 Cashdan, E. (1993) Attracting mates: effects of paternal investment on mate attraction strategies. *Ethol. Sociobiol.* 14, 1–23

35 Hewlett, B. *et al.* (2000) Parental investment strategies among Aka foragers, Ngandu farmers, and Euro–American urban industrialists. In *Adaptation and Human Behavior: An Anthropological Perspective* (Cronk, L. *et al.*, eds), pp. 149–172, Aldine de Gruyter

36 Daly, M. and Wilson, M. (1988) *Homicide*, Aldine de Gruyter

37 Hurtado, A.M. *et al.* (1992) Trade-offs between female food acquisition and child care among Hiwi and Ache foragers. *Hum. Nat.* 3, 185–216

38 Hawkes, K. (1993) Why hunter–gatherers work. *Curr. Anthropol.* 34, 341–362

39 Bliege Bird, R. (1999) Cooperation and conflict: the behavioral ecology of the sexual division of labor. *Evol. Anthropol.* 8, 65–75

40 Smith, E.A. and Bliege Bird, R.L. (2000) Turtle hunting and tombstone opening: Public generosity as costly signaling. *Evol. Hum. Behav.* 21, 245–261

41 Bliege Bird, R. *et al.* The hunting handicap: Costly signaling in human male foraging strategies. *Behav. Ecol. Sociobiol.* (in press)

42 Voland, E. (1998) Evolutionary ecology of human reproduction. *Annu. Rev. Anthropol.* 27, 347–374

43 Bowlby, J. (1969) *Attachment*, Basic Books

44 Foley, R. (1996) The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. *Evol. Anthropol.* 4, 194–203

45 Irons, W. (1998) Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evol. Anthropol.* 6, 194–204

46 Strassman, B.I. and Dunbar, R.I. (1999) Human evolution and disease: Putting the stone age in perspective. In *Evolution in Health and Disease* (Stearns, S.C., ed.), pp. 91–101, Oxford University Press

47 Richerson, P.J. and Boyd, R. (1992) Cultural inheritance and evolutionary ecology. In *Evolutionary Ecology and Human Behavior* (Smith, E.A. and Winterhalder, B., eds), pp. 61–92, Aldine de Gruyter

48 Turke, P.W. (1990) Which humans behave adaptively, and why does it matter? *Ethol. Sociobiol.* 11, 305–339

49 Crawford, C.B. (1993) The future of sociobiology: counting babies or studying proximate mechanisms. *Trends Ecol. Evol.* 8, 183–186

50 Tooby, J. (1999) Quoted in 'For our ancestors, taking risks was a good bet.' *Time Magazine* 154, 6 September 1999

51 Borgerhoff Mulder, M. (1998) The demographic transition: are we any closer to an evolutionary explanation? *Trends Ecol. Evol.* 13, 266–270

52 Daly, M. and Wilson, M. (1994) Evolutionary psychology of male violence. In *Male Violence* (Archer, J., ed.), pp. 253–288, Routledge

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

54 Clutton-Brock, T.H. and Parker, G.A. (1995) Punishment in animal societies. *Nature* 373, 209–216

55 CIBA Foundation, ed. (1997) *Characterizing Human Psychological Adaptations*, John Wiley & Sons

56 Gigerenzer, G. *et al.* (1999) *Simple Heuristics That Make Us Smart: Evolution and Cognition*, Oxford University Press

57 Hill, K. and Kaplan, H. (1999) Life history traits in humans: theory and empirical studies. *Annu. Rev. Anthropol.* 28, 397–430

58 Jones, D. (1999) Evolutionary psychology. *Annu. Rev. Anthropol.* 28, 553–575

59 Cronk, L. *et al.*, eds (2000) *Adaptation and Human Behavior: An Anthropological Perspective*, Aldine de Gruyter

Reducing the genome size of organelles favours gene transfer to the nucleus

Marc-André Selosse, Béatrice Albert and Bernard Godelle

Endosymbiotic organelles exhibit strong genetic erosion during their evolution as a result of the loss of unnecessary genes and of gene transfer to the nucleus. The reasons for this erosion are much debated. Unidirectionality of DNA exchange between cell compartments could favour biased gene transfer, but selection might also act to favour nuclear localization of genes, for example, because organelles accumulate more mutations than do nuclei. Selection for rapid replication might be a general cause of organelle genome reduction. This selection also accounts for the compactness of organelle genomes.

Mitochondria and plastids are remnants of free-living organisms, engulfed in the eukaryotic cell[1], whose genome has been drastically eroded. The various plastid lineages have lost >95% of the gene content present in free-living cyanobacteria[2] (Table 1). The genome is even smaller in animal mitochondria (about 50 kb, 100-fold less than in free-living bacteria), whereas it is entirely lost in hydrogenosomes, recently been demonstrated to be the modified mitochondria of anaerobic eukaryotes[3].

The genes missing from endosymbiotic organelles have been either lost or transferred. Some genes were lost because they became dispensable (such as those required for cell-wall building or motility), and others were lost because nuclear genes took over their function (gene 'transfer'), as described for some plastid ribosomal proteins[4] and for mitochondrial aminoacyl-tRNA synthetase[5]. This transfer corresponds to a series of rare events (Box 1) that replace an organelle gene with a copy of itself, situated in the nucleus of the host and targeting its product to the organelle with a TRANSIT PEPTIDE (see Glossary; Fig. 1). The resulting nucleo-cytoplasmic redundancy is followed by the loss of the organelle gene. Many other organelle genes have been transferred to the nucleus, where they still code for the organelle protein[1] (Fig. 1b) – up to 5000 genes might have been relocated during plastid evolution[2]. An example of a gene transferred from plastids to the nucleus in plants is *rbcS*, the gene encoding the small subunit of the ribulose 1-5-bisphosphate carboxylase oxidase (RuBisCO).

Researchers have examined why organelle genes should stay in organelles[6,7], but have paid less attention to why the organelle genomes should be eroded[2,8,9]. Here, we examine the various hypotheses