ANIMAL BEHAVIOUR, 2000, **60**, F21–F26
doi:10.1006/anbe.2000.1478, available online at http://www.idealibrary.com on IDEAL®

FORUM

Evolutionary analyses of human behaviour: a commentary on Daly & Wilson

ERIC ALDEN SMITH*, MONIQUE BORGERHOFF MULDER† & KIM HILL‡
*Department of Anthropology, University of Washington
†Department of Anthropology, University of California, Davis
‡Department of Anthropology, University of New Mexico

(Received 19 May 1999; initial acceptance 20 August 1999;
final acceptance 13 March 2000; MS. number: AS-1241)

In a recent *Animal Behaviour* review, Daly & Wilson (1999, hereafter D&W) present a stimulating, but in important ways misleading, account of the history and present state of evolutionary analyses of human behaviour. Concerned that those not familiar with this research will be misled by D&W's account, we offer the following commentary. We wish to make three main points: (1) D&W's account is heavily biased toward the theoretical and methodological preferences of one approach to the study of human behaviour and evolution, and underplays or misrepresents other approaches; (2) the approach D&W advocate, evolutionary psychology (EP), suffers from several methodological and conceptual limitations; (3) human behavioural ecology (HBE) provides a complementary approach that avoids these limitations.

Evolutionary Psychology Is a Part, Not the Whole

According to D&W, the field of human evolutionary psychology 'encompasses' the work of all those engaged in evolutionary analyses of human behaviour, 'including even those who have deliberately differentiated themselves from "evolutionary psychology" as "evolutionary anthropologists", "human sociobiologists" and "human behavioural ecologists" ' (page 509). We find this account deficient on three grounds. First, these other fields have a considerably longer history than EP. Because of our own interests and expertise, here we will focus specifically on human behavioural ecology, while recognizing that there are various approaches to evolutionary analysis of human behaviour in such fields as economics, history, philosophy, medicine, literature, sociology, political science and law that neither we nor D&W attempt to review. Research in HBE extends back into the 1970s with articles published in mainstream anthropology journals (e.g. Denham 1971; Wilmsen 1973; Dyson-Hudson & Smith 1978). The early HBE research, while not sophisticated by contemporary standards, drew explicitly on contemporaneous theory in evolutionary ecology (e.g. Brown 1964; MacArthur & Pianka 1966; Orians 1969). Furthermore, from the start this research tested hypotheses about behavioural optimization in response to environmental cues (and not simply that behaviour had 'positive reproductive consequences', as D&W claim).

Second, any 'deliberate differentiation' between EP and these other traditions was in fact initiated a decade ago by certain proponents of EP (e.g. Symons 1989; Tooby & Cosmides 1989). Their attack generated a vigorous rebuttal; D&W cite some of these exchanges, but fail to appreciate the complex and increasingly complementary relationship between these approaches (see Borgerhoff Mulder et al. 1997; Sherman & Reeve 1997; Smith 1998, 2000). Given this history, which can be easily traced in the journal literature, it would be far more accurate to say that EP has 'deliberately differentiated' itself from pre-existing frameworks such as HBE.

Third, turning from historical to theoretical considerations, we question the D&W view that evolutionary psychology 'encompasses' all other evolutionary analyses of human behaviour. While we certainly agree that any analysis of behaviour is 'psychological' in the sense that it incorporates assumptions about information processing and decision making, we think that there are sufficient theoretical and methodological distinctions between HBE and EP to view these as distinct but complementary

Correspondence: E. A. Smith, Department of Anthropology, University of Washington, Box 353100, Seattle, WA 98195, U.S.A. (email: easmith@u.washington.edu). M. Borgerhoff Mulder is at the Department of Anthropology, University of California, Davis CA 95616, U.S.A. K. Hill is at the Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

routes to an evolutionary understanding, in the tradition of Mayr (1976) and Tinbergen (1968). In short, D&W's history of evolutionary research on human behaviour, and of the divergence between EP and HBE, is misleading. While we applaud the recent growth of selectionist perspectives in psychological research, this does not justify subsuming existing or future research in human behavioural ecology under the EP rubric.

Some Contrasts Between EP and HBE

To a considerable extent, EP and HBE are complementary, differing in the relative emphasis placed on psychological mechanism versus manifest behaviour. But EP diverges from HBE in other important and controversial ways, concerning: (1) the use of formal models and deductive theory; (2) emphasis on domain-specific cognitive algorithms; (3) the relationship between psychological mechanisms and observed behaviour; (4) assertions regarding adaptive lag and adaptation to past environments; (5) views on the relevance of fitness measures to analyses of contemporary behaviour. These divergences between EP and HBE have several major consequences for analysis of behaviour of any organism (human or nonhuman).

With respect to the first two contrasts listed, EP insists that all decision mechanisms are domain specific. According to at least some version of EP, it follows from this that the use of optimization models to generate predictions about fitness-maximizing decisions is a form of naïve adaptationism that confuses proximate with ultimate explanation (D&W, page 512). Yet abundant empirical evidence from human and nonhuman behaviour shows that fitness maximization is often a better predictor of behavioural patterns than is pursuit of any one specific goal (which is not to claim that people or other organisms are literally or consciously trying to maximize fitness). This is presumably because nature is full of trade-offs, and organisms have evolved mechanisms to appropriately weight different goals and currencies. While partitioning adaptive problems into 'discrete, real-world problem domains (such as mate value assessment, kin recognition, parental investment allocation, and threat and bluff)' may 'carve the psyche more nearly at its joints' (D&W, page 510), it is not at all clear how EP as presently practised helps us analyse the myriad situations where these domains interact in determining adaptive payoffs. Tackling this latter question is the particular contribution of the optimization and ESS models employed in behavioural ecology (including HBE).

The third difference might appear to be simply a case of complementarity: the central goal of EP is to explain the psychological mechanisms that underlie observed behaviour as devices that were selected to solve adaptive problems in our evolutionary past, whereas HBE attempts to map the correspondence between behavioural variation and immediate social and environmental payoffs. In practice, however, the EP research strategy often ends up simply ascribing behavioural patterns, or verbal statements about preferences, to hypothesized psychological mechanisms (often referred to in the EP literature as 'mental modules' running 'Darwinian algorithms'). The central problem here is that behaviour is unlikely to be a simple expression of evolved psychological mechanisms, but rather a complex outcome of interaction between such mechanisms and psychological, social and cultural dynamics. Indeed, as pointed out by Geoffrey Miller (1997), himself an evolutionary psychologist, more than a decade of research into characterizing the human psychological adaptation underlying men's and women's mating preferences has done little more than generate a list of the sexual and parental cues men look for in women, and vice versa. How are these cues weighted in terms of context, how do they interact with one another, how are they evaluated statistically in the brain, and (most importantly in our view) how are they used in the real world of mating markets and biological clocks? These questions need to be addressed with the life history models and game theoretical approaches used in HBE. At present they remain almost entirely uninvestigated by evolutionary psychologists, even though mate choice is their most heavily worked turf.

The fourth issue on our list concerns a central tenet of EP that one should explain psychological mechanisms as evolved solutions to adaptive problems in the remote past (which, following Bowlby 1969, they term the environment of evolutionary adaptedness, or EEA). In practice, the evolutionary part of EP often reduces to rather vague claims about selective conditions in the EEA that may have favoured the evolution of a hypothesized psychological mechanism. Certainly EP is on safe ground to assume that women rather than men bore the toll of pregnancy and lactation in the EEA, for example; but many EP analyses are based on less secure assumptions about the EEA. As one example, the EP literature on mate choice generally makes assumptions about male provisioning that are currently subject to vigorous debate and weighing of empirical evidence in the HBE literature (e.g. Hawkes et al. 1997; Bliege Bird 1999; Kaplan et al., in press). To the extent that our knowledge of the EEA remains sketchy (Foley 1996), rigorous quantitative testing of precise selectionist hypotheses becomes virtually impossible, and the result can easily degenerate into adaptive storytelling.

While we certainly agree that products of evolution are adapted to past environments, we do not accept without detailed evidence that human phenotypic responses are so inflexible and modern environments so altered that contemporary maladaptation must be common. Yet advocates of the EP paradigm (including D&W at several points) frequently attack as misguided those who do not adopt this particular view of adaptation to the EEA. D&W complain that critics of the EEA concept have reduced it to a caricature (page 513); to the contrary, we believe the critics have in mind the way the concept is usually employed in the EP literature, as one that separates the remote evolutionary past to which our domain-specific mechanisms are unalterably adapted, and the dramatically novel present, in which these mechanisms produce 'mismatches' that 'compromise the effectiveness of human adaptations' (D&W, page 512). Given this conception, it follows that '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' (Symons 1989, pp. 138–139, original emphasis). In contrast, HBE researchers begin with the assumption that evolved conditional strategies, learning biases, and social information transfer will produce adaptive outcomes most of the time, even in relatively novel environments. To the extent that empirical information supports this expectation, it suggests that only the environmental details are novel, not the fundamental trade-offs they present, nor the ability to recognize and appropriately react to those trade-offs.

D&W repeat the common EP assertion that other approaches to human behavioural evolution suffer from hyper-adaptationism and inattention to evolutionary disequilibria or adaptive lag; but like others who have done so, they provide precious little evidence of this. Thus, D&W chastise 'self-styled behavioural ecologists' by quoting Kacelnik & Krebs's (1997) analogy between human behaviour in modern contexts and the insect-eating behaviour of trout in a stream with anglers and artificial flies, both evidently maladaptative. But are they? We suggest it would be more useful, in the case of trout, first to ask whether the costs of predation by modern anglers are outweighed by the benefits of the insect food consumed to fish attracted to flashing wings on the water surface. HBE (but not EP) offers a theoretical and methodological framework for posing and answering such questions, by predicting and measuring the fitness-related costs and benefits that arise from such trade-offs. To simply assert that behaviour in a novel environment is maladaptive, as evolutionary psychologists have done for a variety of human traits, offers little analytical insight into the design of evolved mechanisms or behavioural phenotypes, whether trout or human. All organisms face trade-offs, and all traits exact costs; pointing to the negative side of a given trade-off, or noting that costs have likely increased in a novel environment, does not provide valid grounds for concluding that the trait is maladaptative.

How does one evaluate the claim that adaptive lag 'might have destroyed any association between reproductive success differentials and the proper functioning of psychological adaptations' (D&W, page 513)? Because EP pronounces measurement of the fitness consequences irrelevant to selectionist analysis in modern societies, it asks us to accept its claims about pervasive adaptive lag on faith. To the contrary, we assert that while adaptive lag is a real possibility, to take its measure we need to move beyond just-so stories to rigorous hypothesis testing in the tradition of behavioural ecology. The phenomenon of fertility reduction via contraceptive technology in modern society provides an instructive example. D&W (page 513) simply assume it is maladaptive (as is commonly done in the EP literature), and offer no explanation of its occurrence or variation. In contrast, human behavioural ecologists take a number of analytical steps. They start by investigating whether the behaviour is currently adaptive. If it is not, they attempt to identify what precisely has changed in the environment to produce the maladapative outcome, and employ optimization models and life history theory to address why this might be the case. They also hypothesize about the proximate mechanisms that would have led to optimal fertility decisions in previous historical environments but nonoptimal fertility in the present context. Finally, they design empirical studies to test these hypotheses, using comparative data whenever possible. These investigations have succeeded in revealing the complex relationships between investment in offspring and wealth and other economic constraints, and directly explain why wealth is not linearly related to reproduction even in nonmodern societies (e.g. Rogers 1995; Kaplan 1996; Borgerhoff Mulder 1998; Mace 1998).

Our fifth issue concerns EP arguments, repeated by D&W, that fitness measures are irrelevant to evolutionary analyses of current behaviour. As these arguments have recently been discussed in detail elsewhere (Borgerhoff Mulder et al. 1997; Sherman & Reeve 1997; Smith 1998), we will be relatively brief. There are certainly times when measuring fitness or its components (e.g. reproductive success, survivorship) is too difficult, unlikely to discriminate finely (e.g. in short-term decision-making contexts), or otherwise inappropriate. But these are not grounds for the blanket rejection of fitness measures advocated by D&W and others; nor is the reliance of some HBE research on such measures (along with many other measures, including mating frequencies, energy consumption rates, etc.) tantamount to assuming that individuals have 'a magic ability to find the course of action that maximizes inclusive fitness' (D&W, page 512). True, the HBE research strategy (see below) starts with the assumption that organisms will behave as if they have that 'magic ability', but this is a means of formulating hypotheses about phenotypic design, not an article of faith, and certainly not some confusion about 'inclusive fitness as a motive or objective' (ibidem). Furthermore, in our experience the fitness-maximization assumption usually comes closer to predicting observed behaviour than an assumption that fitness consequences are irrelevant.

EP researchers are all too ready to assume that a given trait maximized fitness in the EEA (a truly untestable assertion) even as they find fitness measures irrelevant in the present. For example, in a discussion of what they term 'the young male syndrome', Daly & Wilson (1994, page 278) propose that 'competitive success or failure in early adulthood has been an especially strong determinant of total lifetime fitness in men'. Here (as elsewhere in the EP literature), the allegation of past fitness effects is used to justify hypotheses about the design features of contemporary behaviour. That is fine as far as it goes, but to rule out any contemporary investigation of fitness outcomes produces a truncated analysis based on the weakest possible link to selection pressures (i.e. those hypothesized to have occurred in remote and unobservable times). Whatever the dangers of over-reliance on fitness measures in testing evolutionary hypotheses about behaviour, they do not justify the total ban advocated by evolutionary psychologists. In the terminology of Sherman & Reeve (1997), both 'forward' (from postulated selective environments to expected behaviour) and 'backward' (from observed behaviour and associated fitness consequences to postulated selective environments) approaches have complementary strengths and weaknesses, dependent largely on the particular research problem being investigated.

What Does Human Behavioural Ecology Offer?

Daly & Wilson present their review as inclusive of human behavioural ecology, but in fact ignore most of the HBE literature, with only a dozen of their 134 citations being HBE research. (For reviews of this literature, see Borgerhoff Mulder 1988, 1991; Cronk 1991; Smith 1992a, b; Voland 1998; Winterhalder & Smith 2000; and the volumes edited by Smith & Winterhalder 1992 and Cronk et al. 2000.)

Whereas EP researchers are primarily interested in characterizing pan-human psychological mechanisms, the HBE approach (following the general behavioural ecology paradigm) focuses on explaining variation in behaviour as a function of ecological and social context and the resulting adaptive payoffs. This research strategy can be outlined in ideal form as follows. First, we use theory to deduce the likely functional relationships (F1s) between behavioural alternatives and their associated costs and benefits in some proximate and measurable currencies. We then theorize how those relationships might change as a function of a variety of ecological variables that we suspect are related to behavioural variation. We also develop expectations about the relationships between the proximate currencies and overall fitness outcomes (F2s), another set of functions which may vary with ecology. These functional relationships will determine the behaviour that provides the highest genetic contribution under any given ecology. We then attempt to empirically verify that F1s and F2s take the hypothesized shape (or go right to this step when we have no good theory about these functions). Finally, we describe what an optimal response would be in a variety of ecologies, assuming a perfectly designed organism (the maximum net benefit in each ecology given F1 and F2), and compare this to observed behaviour to determine how close it comes to predicted optima. This provides one route to uncovering the mechanism or phenotypic design that has actually evolved (rather than the hypothesized optimal solution). We may find that individuals lack the ability to vary behaviour optimally along some dimension, and try to determine why. For example, they may behave as if F1 and F2 are simpler functions than they really are; or they may not take into account F1 or F2 functions outside the range experienced in the population's evolutionary history (the adaptive lag with which EP is so concerned).

As noted above, research in HBE began in the 1970s, and in the first decade or so was heavily focused on foraging strategies (reviews in Smith 1983; Kaplan & Hill 1992). Early work studied prey choice, patch use, group size and time allocation. As attention turned towards such factors as risk, exchange and multiple currencies, the analytical sophistication increased (e.g. Winterhalder 1986, 1996; Hill 1988; Cashdan 1990; Hawkes 1991). Beginning somewhat later than the foraging-focused research, HBE researchers began analysing mating and parental behaviour (reviews in Borgerhoff Mulder 1992; Cronk et al. 2000).

Current HBE research maintains the research strategy discussed above, but has diversified into a wide range of substantive topics, including analyses of human life history strategies, menopause and senescence (e.g. Hill 1993; Rogers 1993; Hill & Hurtado 1996; Hawkes et al. 1997, 1998; Wilson & Daly 1997); trade-offs between reproduction and parental investment (e.g. Hawkes et al. 1995; Rogers 1995; Kaplan 1996; Borgerhoff Mulder 1998; Bliege Bird 1999; Blurton Jones et al. 2000; Kaplan et al., in press); sex-biased parental investment and reproductive competition within families (e.g. Hrdy & Judge 1993; Smith & Smith 1994; Strassman 1997; Borgerhoff Mulder 1998; Voland 1998); resource conservation (e.g. Alvard 1998; Winterhalder & Lu 1998; Ruttan & Borgerhoff Mulder 1999); and status competition via costly signalling (e.g. Boone 1998; Neiman 1998; Smith & Bliege Bird, in press), to mention a few. Following the example of work in nonhuman behavioural ecology, HBE increasingly employs ESS models (e.g. Ruttan & Borgerhoff Mulder 1999), dynamic programming (e.g. Mace 1996; Luttbeg et al. 2000) and multivariate statistical control over phenotypic correlations (e.g. Hill & Hurtado 1996) and phylogenetic bias (e.g. Cowlishaw & Mace 1996).

In conclusion, while we have great respect for Daly & Wilson's own research, we strongly question several key elements of their essay, and some aspects of the evolutionary psychology framework they so forcefully advocate. We fully support a pluralistic research strategy in evolutionary analyses of human behaviour, and recognize the valuable contribution evolutionary psychology can make, in conjunction with more behavioural and ecological approaches. But we reject the exclusionary attitude of many evolutionary psychologists that theirs is the only valid approach, an attitude we doubt Daly & Wilson share, but one encouraged by their proposal to subsume all evolutionary analyses of human behaviour under the term 'Human Evolutionary Psychology.' We urge readers of *Animal Behaviour* to examine the HBE literature (among others) to ensure a more balanced understanding of the state of the art in evolutionary analyses of human behaviour than provided by the essay we have criticized here.

We thank Sarah Blaffer Hrdy, Bruce Winterhalder, Paul Sherman, Ed Hagen and two anonymous referees for useful advice, not always heeded; and Martin Daly and Margo Wilson for remaining collegial despite our criticisms of their essay.

References

Alvard, M. S. 1998. Evolutionary ecology and resource conservation. *Evolutionary Anthropology*, **7**, 62–74.

Bliege Bird, R. 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. *Evolutionary Anthropology*, **8**, 65–75.

Blurton Jones, N., Marlowe, F. W., Hawkes, K. & O'Connell, J. F. 2000. Paternal investment and hunter-gatherer divorce rates. In: *Adaptation and Human Behavior: an Anthropological Perspective* (Ed. by L. Cronk, N. Chagnon & W. Irons), pp. 65–86. Hawthorne, New York: Aldine de Gruyter.

Boone, J. L. 1998. The evolution of magnanimity: when is it better to give than to receive? *Human Nature*, **9**, 1–21.

Borgerhoff Mulder, M. 1988. Behavioural ecology in traditional societies. *Trends in Ecology and Evolution*, **3**, 260–264.

Borgerhoff Mulder, M. 1991. Human behavioural ecology. In: *Behavioural Ecology: an Evolutionary Approach*. 3rd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 69–98. Oxford: Blackwell.

Borgerhoff Mulder, M. 1992. Reproductive decisions. In: *Evolutionary Ecology and Human Behavior* (Ed. by E. A. Smith & B. Winterhalder), pp. 339–374. Hawthorne, New York: Aldine de Gruyter.

Borgerhoff Mulder, M. 1998. Demographic transition: are we any closer to an evolutionary explanation? *Trends in Ecology and Evolution*, **13**, 266–270.

Borgerhoff Mulder, M., Richerson, P. J., Thornhill, N. & Voland, E. 1997. The place of behavioral ecological anthropology in the evolutionary social sciences. In: *Human By Nature: Between Biology and the Social Sciences* (Ed. by P. Weingart, S. D. Mitchell, P. J. Richerson & S. Maasen), pp. 253–282. Hillsdale, New Jersey: L. Erlbaum.

Bowlby, J. 1969. *Attachment*. New York: Basic Books.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin*, **76**, 160–169.

Cashdan, E. A. (Ed.) 1990. *Risk and Uncertainty in Tribal and Peasant Economies*. Boulder, Colorado: Westview Press.

Cowlishaw, G. & Mace, R. 1996. Cross-cultural patterns of marriage and inheritance: a phylogenetic approach. *Ethology and Sociobiology*, **17**, 87–97.

Cronk, L. 1991. Human behavioral ecology. *Annual Review of Anthropology*, **20**, 25–53.

Cronk, L., Chagnon, N. & Irons, W. (Eds) 2000. *Human Behavior and Adaptation: an Anthropological Perspective*. Hawthorne, New York: Aldine de Gruyter.

Daly, M. & Wilson, M. 1994. Evolutionary psychology of male violence. In: *Male Violence* (Ed. by J. Archer), pp. 253–288. London: Routledge.

Daly, M. & Wilson, M. 1999. Human evolutionary psychology and animal behaviour. *Animal Behaviour*, **57**, 509–519.

Denham, W. W. 1971. Energy relations and some basic properties of primate social organization. *American Anthropologist*, **73**, 77–95.

Dyson-Hudson, R. & Smith, E. A. 1978. Human territoriality: an ecological reassessment. *American Anthropologist*, **80**, 21–41.

Foley, R. A. 1996. The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. *Evolutionary Anthropology*, **4**, 194–203.

Hawkes, K. 1991. Showing off: tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology*, **12**, 29–54.

Hawkes, K., Rogers, A. R. & Charnov, E. L. 1995. The male's dilemma: increased offspring production is more paternity to steal. *Evolutionary Ecology*, **9**, 662–677.

Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Current Anthropology*, **38**, 551–577.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H. & Charnov, E. L. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 1336–1339.

Hill, K. 1988. Macronutrient modifications of optimal foraging theory: an approach using indifference curves applied to some modern foragers. *Human Ecology*, **16**, 157–197.

Hill, K. 1993. Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, **2**, 78–88.

Hill, K. & Hurtado, A. M. 1996. *Ache Life History: the Ecology and Demography of a Foraging People*. Hawthorne, New York: Aldine de Gruyter.

Hrdy, S. B. & Judge, D. S. 1993. Darwin and the puzzle of primogeniture: an essay on biases in parental investment after death. *Human Nature*, **4**, 1–45.

Kacelnick, A. & Krebs, J. 1997. Yanomamö dreams and starling payloads: the logic of optimality. In: *Human Nature: a Critical Reader* (Ed. by L. M. Betzig), pp. 70–72. New York: Oxford University Press.

Kaplan, H. 1996. A theory of fertility and parental investment in traditional and modern human societies. *Yearbook of Physical Anthropology*, **39**, 91–135.

Kaplan, H. & Hill, K. 1992. The evolutionary ecology of food acquisition. In: *Evolutionary Ecology and Human Behavior* (Ed. by E. A. Smith & B. Winterhalder), pp. 167–201. Hawthorne, New York: Aldine de Gruyter.

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. In press. A theory of human life history evolution: diet, intelligence and longevity. *Evolutionary Anthropology*.

Luttbeg, B., Borgerhoff Mulder, M. & Mangel, M. 2000. To marry again or not: a dynamic model for demographic transition. In: *Adaptation and Human Behavior: an Anthropological Perspective* (Ed. by L. Cronk, N. Chagnon & W. Irons), pp. 345–368. Hawthorne, New York: Aldine de Gruyter.

MacArthur, R. H. & Pianka, E. R. 1966. On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.

Mace, R. 1996. When to have another baby: a dynamic model of reproductive decision-making and evidence from Gabbra pastoralists. *Ethology Sociobiology*, **17**, 263–273.

Mace, R. 1998. The coevolution of human fertility and wealth inheritance strategies. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 389–397.

Mayr, E. 1976. Cause and effect in biology. In: *Evolution and the Diversity of Life* (Ed. by E. Mayr), pp. 359–371. Cambridge, Massachusetts: Harvard University Press.

Miller, G. F. 1997. Mate choice: from sexual cues to cognitive adaptations. In: *Characterizing Human Psychological Adaptations* (Ed. by G. Bock & G. Cardew), pp. 71–82. Chichester: J. Wiley.

Neiman, F. D. 1998. Conspicuous consumption as wasteful advertising: a Darwinian perspective on spatial patterns in Classic Maya terminal monument dates. In: *Rediscovering Darwin: Evolutionary Theory and Archeological Explanation* (Ed. by C. Michael Barton & Geoffrey A. Clark), pp. 267–290. Washington, D.C.: American Anthropological Association.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist*, **103**, 589–603.

Rogers, A. R. 1993. Why menopause? *Evolutionary Ecology*, **7**, 406–420.

Rogers, A. R. 1995. For love or money: the evolution of reproductive and material motivation. In: *Human Reproductive Decisions: Biological and Social Perspectives* (Ed. by R. I. M. Dunbar), pp. 76–95. London: Macmillan.

Ruttan, L. M. & Borgerhoff Mulder, M. 1999. Wealth asymmetries and grazing restraint among East African pastoralists. *Current Anthropology*, **40**, 621–652.

Sherman, P. & Reeve, H. 1997. Forward and backward: alternative approaches to studying human social evolution. In: *Human Nature: a Critical Reader* (Ed. by L. M. Betzig), pp. 147–158. New York: Oxford University Press.

Smith, E. A. 1983. Anthropological applications of optimal foraging theory: a critical review. *Current Anthropology*, **24**, 625–651.

Smith, E. A. 1992a. Human behavioral ecology I. *Evolutionary Anthropology*, **1**, 20–25.

Smith, E. A. 1992b. Human behavioral ecology II. *Evolutionary Anthropology*, **1,** 50–55.

Smith, E. A. 1998. Is Tibetan polyandry adaptive? Methodological and metatheoretical analyses. *Human Nature*, **9,** 225–261.

Smith, E. A. 2000. Three styles in the evolutionary study of human behavior. In: *Human Behavior and Adaptation: an Anthropological Perspective* (Ed. by L. Cronk, W. Irons & N. Chagnon), pp. 25–44. Hawthorne, New York: Aldine de Gruyter.

Smith, E. A. & Bliege Bird, R. L. In press. Turtle hunting and tombstone opening: public generosity as costly signaling. *Evolution and Human Behavior*, **21**.

Smith, E. A. & Smith, S. A. 1994. Inuit sex ratio variation: population control, ethnographic artifact, or parental manipulation? *Current Anthropology*, **35,** 595–624.

Smith, E. A. & Winterhalder, B. (Eds) 1992. *Evolutionary Ecology and Human Behavior*. Hawthorne, New York: Aldine de Gruyter.

Strassman, B. I. 1997. Polygyny as a risk factor for child mortality among the Dogon. *Current Anthropology*, **38,** 688–695.

Symons, D. 1989. A critique of Darwinian anthropology. *Ethology and Sociobiology*, **10,** 131–144.

Tinbergen, N. 1968. On war and peace in animals and man. *Science*, **160,** 1411–1418.

Tooby, J. & Cosmides, L. 1989. Evolutionary psychology and the generation of culture, part I: theoretical considerations. *Ethology and Sociobiology*, **10,** 29–49.

Voland, E. 1998. Evolutionary ecology of human reproduction. *Annual Review of Anthropology*, **27,** 347–374.

Wilmsen, E. N. 1973. Interaction, spacing behavior, and the organization of hunting bands. *Journal of Anthropological Research*, **29,** 1–31.

Wilson, M. & Daly, M. 1997. Life expectancy, economic inequality, homicide, and reproductive timing in Chicago neighbourhoods. *British Medical Journal*, **314,** 1271–1274.

Winterhalder, B. 1986. Optimal foraging: simulation studies of diet choice in a stochastic environment. *Journal of Ethnobiology*, **6,** 205–223.

Winterhalder, B. 1996. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology*, **5,** 46–57.

Winterhalder, B. & Lu, F. 1998. A forager-resource population ecology model and implications for indigenous conservation. *Conservation Biology*, **11,** 1354–1364.

Winterhalder, B. & Smith, E. A. 2000. Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evolutionary Anthropology*, **9,** 51–72.