Why mechanisms shouldn't be ignored

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Commentary on Nettle et al. 'Human behavioural ecology: current research and future prospects'

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The article by Nettle and colleagues provides a broad and comprehensive summary of the field of *human behavioural ecology* (HBE). Alongside the fields of *evolutionary psychology* and *cultural evolution*, HBE is currently one of the dominant contemporary approaches within the human evolutionary behavioural sciences (Laland and Brown 2011). Since the 1970s, HBE has provided novel and compelling explanations for a range of behaviour patterns, including foraging strategies, mating decisions and parental investment, and has used optimality models to provide a clearer understanding human life history trade-offs. The authors have collated over 350 HBE studies, indicating that the field is thriving. Here, I comment on the observation that HBE methods are increasingly being applied to industrialised societies and then provide a counter-argument to the authors' suggestion that culture can be treated just like any other proximate mechanism.

One of the strengths of HBE has been the use of detailed, long-term databases, which provide rich sources of information on numerous aspects of behaviour, social structure and life history, allowing researchers to test models against real-world scenarios. Such databases, which are time-consuming to produce and analyse, add rigour to the field of HBE. During the

early phases of HBE, most studies were carried out on foragers or small-scale subsistence populations, based on the assumption that optimality models would be more readily applicable to such populations (Borgerhoff Mulder and Schacht 2012). However, Nettle and colleagues have shown that HBE has expanded its remit by testing whether optimality approaches can also shed light on behaviour and life history within industrialised populations. The successful application of HBE approaches to datasets from industrialised populations supports the argument that the amount of adaptive lag (or 'mismatch') experienced by human beings has been overstated (Laland and Brown 2006). In addition, such research upholds the argument that a clearer understanding of cross-cultural behavioural diversity will be provided by moving away from a focus on universal traits (Brown et al. 2009; 2011).

In their 'Open questions' section, the authors point out that HBE remains generally agnostic with regard to the mechanisms by which human beings end up exhibiting adaptive behaviour patterns, e.g. via transmitted culture or evolved predispositions. They argue that HBE methods can be successfully applied without a need to understand the underlying mechanisms, and that an understanding of mechanisms is required only when predictions from optimality models fail to be upheld. Where the models are not successful, the authors suggest that the study of mechanisms could reveal either evolved cognitive constraints or the spread of maladaptive cultural traits. Although I agree that adopting the phenotypic gambit has the benefit of keeping HBE models simple, I would argue (alongside other behavioural ecologists, e.g. McNamara and Houston 2009; Fawcett et al. 2012) that a more complete understanding of behaviour can be gained by including questions about mechanisms from the start, above and beyond the revealing of constraints and maladaptive outcomes. Culture, in particular, brings added complexities to human behaviour, and I present two points in favour of incorporating the study of cultural processes more extensively into HBE research.

Firstly, by taking an a-historic perspective, HBE models are potentially unable to explain why humans in a particular population occupy one out of a multitude of adaptive peaks. By ignoring the role of cultural transmission and other historical processes, HBE models thus provide only a partial explanation for why a population exhibits a particular behaviour pattern. The authors' suggestion that an understanding of cultural mechanisms is only required when behaviour departs from optimality misses the point that the cultural history of a population has a major impact upon which behaviour patterns are adopted. Examining the role of cultural processes can provide valuable insights into behaviour and reveal how populations can reach novel adaptive equilibria (Richerson and Boyd 2005). To the extent that HBE models are increasingly taking cultural processes into account (e.g., Borgerhoff Mulder et al. 2009; Mace and Jordan 2011), a closer integration between HBE and cultural evolution models is already enhancing our understanding of human behaviour. The key point here is that, by incorporating cultural transmission into its analyses, HBE can go beyond assessing whether human behaviour is adaptive to (i) predict more effectively which adaptive solutions particular populations will adopt, and (ii) explain how the population reached that solution.

Secondly, an a-historic perspective also potentially shields researchers from the notion that human populations have (at least) two inheritance systems, genetic inheritance and cultural inheritance, and that the interactions between these inheritance systems can lead to novel patterns of selection (Boyd and Richerson 1985; Odling-Smee et al. 2003; Laland et al. 2011). Selection pressures acting on human populations are not static, but consist of complex feedback interactions between inheritance systems, and, as Nettle and colleagues point out, cultural transmission can affect the dynamics of adaptive change. To take the example used by the authors, the low fertility rate observed in industrial populations that have undergone the demographic transition is not easily explained using simple optimality models. While the authors suggest that the only answer is to invoke a mismatch between current conditions and

those in which decision-making processes evolved, a cultural evolution perspective, which includes questions about how genetic and cultural inheritance systems interact, could provide a deeper understanding of departures from apparent optima (e.g., Borenstein et al. 2006; Newson and Richerson 2009). When gene-culture coevolution takes place, the currency of evolution changes, and researchers need to consider the fittest of gene-culture combinations (Richerson and Boyd 2005); the fittest gene-culture combinations might not be those associated with the fittest genotypes.

In summary, Nettle and colleagues have provided a thorough and commendable overview of HBE. I agree with the authors that applying optimality approaches to human behaviour can shed light on behavioural variation within and between populations and that this should not be the end point of such investigations. However, I would support a greater integration of questions about mechanisms, particularly those related to transmitted culture, into HBE and of mechanistic questions into behavioural ecology more generally.

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