in-depth explorations of how behavioral processes help generate these effects (an area where these data sets are limited because of the cost of repeated sampling). It is imperative, then, that HBE should strive to maintain the pluralist approach that has characterized its success to date and not privilege any one approach over another.

ADDING HISTORY TO THE BEHAVIORAL GAMBIT

One final point we'd like to raise concerns the phenotypic and behavioral gambits (Fawcett et al., 2012). There is no arguing with the fact that humans dominate the planet, and our unprecedented flexibility could be taken to suggest that general constraints on human behavior, whether genetic, physiological, or psychological in origin, are less stringent than those that affect other animal species. One could argue, therefore, that adopting the phenotypic and behavioral gambits is really quite sensible when it comes to human behavior. Having said this, it is apparent that human behavior does not always conform to theory and may even be maladaptive, suggesting there are, in fact, constraints operating. Our way of reconciling these 2 somewhat contradictory statements is to suggest that constraints may be local, contingent, and peculiar to the population in question and not only a reflection of general constraints common to all humans.

More specifically, a population's (and often species') history may generate constraints in an unpredictable fashion that either are not readily identified using a BE approach or go unrecognized. If we take an animal example (at the risk of seeming to flirt potentially with our self-identified disco problem), it has been shown that, among southern chacma baboons, the concession of reproductive opportunities to subordinates by alpha males can only be understood as the result of a cascading sequence of events that stem from high rates of infanticide in the population, as compared with northern yellow and olive baboon populations (Henzi et al. 2010). This, in turn, likely reflects historic climatic effects that limited male cohort size, in ways that prevented selection for male–male coalition formation, and so increased the likelihood of infanticide as a successful male strategy. In other words, variation in male mating strategies across baboon populations cannot be understood simply as a plastic response to local ecology, as formerly supposed, but needs to be placed in its historical context, with a recognition that this has led to qualitatively different evolutionary solutions. In this way, unique historical events, in this case climatic, may result in flexible behavioral responses that nonetheless retain the signature of these events through time.

Ironically, because of the extreme flexibility of humans, our own actions may sometimes be a source of historical "accidents" of this kind. Thus, although we are sufficiently flexible to arrive at an adaptive solution to unpredictable and contingent events, these may continue to exert a strong influence on future behavioral trajectories because of the manner in which local cultural practices "stick" once they are entrenched and valued by a given society (e.g., Aunger 1994). Consequently, human populations may not currently display the predicted pattern for a given environment because the range of strategies available after such events becomes "culturally canalized" (potentially leading to less than optimal behavior). By the same token, of course, they may also give rise to solutions that are somewhat "messy" and convoluted but nevertheless fitness enhancing. In essence, what we are (tentatively) suggesting is that, although we can play the phenotypic and behavioral gambits with a certain degree of insouciance, we ignore history at our peril.

Address correspondence to L. Barrett. E-mail: louise.barrett@uleth.ca.

Received 17 December 2012; accepted 27 December 2012.

doi: 10.1093/beheco/ars231

Advance Access publication 22 January 2013

Forum editor: Sue Healy

REFERENCES

Aunger R. 1994. Are food avoidances maladaptive in the Ituri forest of Zaire. J Anthrop Res. 50:277–310.
Braithwaite J. 2008. Lekking displays in contemporary organizations: ethologically oriented, evolutionary and cross-species accounts of male dominance. J Health Organ Manage. 22:529–559.
Fawcett TW, Hamblin S, Giraldeau L-A. 2012. Exposing the behavioral gambit: the evolution of learning and decision rules. Behav Ecol. 24:2–11.
Hendrie CA, Mannion HD, Godfrey GK. 2009. Evidence to suggest that nightclubs function as human sexual display grounds. Behaviour. 146:1331–1348.
Henzi SP, Clarke PMR, Pradhan G, van Schaik CP, Barrett L. 2010. Infanticide and reproductive restraint in a polygynous social mammal. Proc Natl Acad Sci USA. 107:2130–2135.
Lycett JEL, Dunbar RIM. 2000. Mobile phones as lekking devices among human males. Human Nature. 11:93–104.
Nettle D, Gibson MA, Lawson DW, Sear R. 2013. Human behavioral ecology: current research and future prospects. Behav Ecol. 34:1031–1040.
West SA, El Mouden C, Gardner A. 2011. Sixteen common misconceptions about the evolution of cooperation in humans. Evol Hum Behav. 32:231–262.
Wiley RH. 1991. Lekking in birds and mammals: behavioural and evolutionary issues. Adv Stud Behav. 20:201–291.

Response: how much you need to engage with mechanism depends on what you are trying to do

Daniel Nettle,[a] Mhairi A. Gibson,[b] David W. Lawson,[c] and Rebecca Sear[d]

[a]Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle upon Tyne NE1 7RU, UK, [b]Department of Archaeology and Anthropology, University of Bristol, 43 Woodland Road, Bristol BS8 1UU, UK, [c]Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK, and [d]Department of Population Health, London School of Hygiene and Tropical Medicine, Keppel Street, London WC1E 7HT, UK

We would like to thank our 4 sets of commentators for their stimulating and supportive words (Barrett and Stulp 2013; Borgerhoff Mulder 2013; Brown 2013,;West and Burton-Chellew 2013). Their reactions to our invited review (Nettle et al. 2013) give us some hope that our characterization of the field was not wildly off the mark and confirm our belief that the issues we identified in our paper as open questions really are open questions. We agree with many of the points raised and will not repeat them one by one here. A major theme that arises from all of them is that behavioral ecology (BE), perhaps of humans in particular, cannot afford to ignore the mechanisms by which behaviors are acquired. We would like to make 3 points about this position.

The first is that mechanism is a Chinese box. Advocates of cultural evolution models argue that these are more realistic than traditional optimality models because they take account of the mechanisms by which behavioral strategies are acquired. However, these models ignore the details of the cognitive science involved in learning, though these details could matter a lot for the outcomes

you get. Cognitive science in turn does not delve into the systems neuroscience of how the brain actually implements learning algorithms. Systems neuroscience takes the neuron as a black box and does not engage with the biochemical processes within the cell, though the exact properties of these could make a lot of difference. In practice, then, every subdiscipline is seen as mechanistically agnostic by the subdiscipline below it in the hierarchy of biological organization. We are sure that no one would advocate that all studies of behavior should begin at the level of the potassium channel. It follows that the science of behavior must, therefore, always be a multimethod, multilayered enterprise with interesting dialogues and interactions between layers. The phenotypic gambit indeed entails a risk and so parallel, or better yet integrated, research on the mechanisms that guide behavior is always desirable. But regardless of which level of analysis a researcher seeks to understand, basic BE data on environment–behavior relationships and the fitness outcomes of alternative strategies will always be an essential foundation of evolutionary research on humans.

The second point is that the extent to which researchers have to engage with mechanism depends in part on what question they are seeking to answer. The overall explanatory goal of BE/HBE can be decomposed into a number of subgoals. For example, sometimes researchers simply want to know what the relationship is between some phenotypic trait—say status, personality, or physical stature—and reproductive success. Here, you just need a good measure of the trait and a good measure of reproductive success, though an estimate of heritability is also useful to predict the response to selection. Sometimes researchers want to know what the optimal behavior in a particular socioecology would be in terms of maximizing inclusive fitness and ask whether their study population is doing it (the answer may often be no, but could sometimes be yes). Here, they need a good optimality model and good characterizations of the socioecology and the behavior. At other times, though, researchers may want to answer a more global question such as "why did the demographic transition occur?" and "why do European societies have enforced monogamy?" We agree that for these kinds of questions, understanding history and of mechanism are going to be crucial. Thus, human behavioral ecologists will need to engage with mechanism at different levels and to differing extents depending on what the exact question is.

Our third point is that there are resources available in humans that offer exciting possibilities for the study of mechanism as well as function. Although we agree with Barrett and Stulp (2013) that humans have obvious limitations as a study species, they have some notable advantages too. Humans are the most studied species on the planet. The problem of integrating mechanisms into HBE, therefore, may partially be solved by a greater integration with the wealth of data, expertise, and empirical research that already exists in the cognitive, social, and medical sciences. To give a few examples, psychologists and neuroscientists can help us understand cognitive mechanisms; demographers and physiologists the nuts and bolts of reproductive function, including hormonal mechanisms; sociologists and anthropologists (at least those committed to a basically scientific approach) sociocultural mechanisms; archaeologists and historians historical detail. This work includes a range of methodologies that speak to several different levels of mechanism. Some of these methodologies are denied to animal BE, and certainly there are few species on which so much data of so many different kinds exist. For those questions where mechanism is important, HBE is perhaps relatively fortunate among BE in having the opportunity to integrate its own work into this existing (and ongoing) body of knowledge.

We conclude by fully supporting Borgerhoff Mulder's (2013) comment that HBE mustn't give up on its traditional strengths of collecting its own data on small-scale societies, while calling for a continued expansion of HBE's boundaries into new methods, topics, and study populations. This will achieve the twin aims of HBE made explicit by Barrett and Stulp (2013): contributing to basic science by adding to the broader field of BE and improving our understanding of human behavior. There is still much to learn about the BE of humans living in "traditional" small-scale societies, in the modern postindustrial world and, perhaps most of all, in those populations in the developing world currently underdoing rapid demographic, economic, and cultural change. Research on the latter, in particular, also has the potential to add a third aim to HBE research: to contribute new insights on how humans interact and respond to their environments to the real world of policy-making, a very significant goal in its own right.

Address correspondence to D. Nettle. E-mail: daniel.nettle@ncl.ac.uk.

Received 18 February 2013; accepted 21 February 2013.

doi:10.1093/beheco/art020

Advance Access publication 27 March 2013

Forum editor: Sue Healy

REFERENCES

Barrett L, Stulp G. 2013. The pleasures and pitfalls of studying humans from a behavioral ecological perspective. Behav Ecol. 34:1045–1046.
Borgerhoff Mulder M. 2013. Human behavioral ecology-necessary but not sufficient for the evolutionary analysis of human behavior. Behav Ecol. 34:1042–1043.
Brown GR. 2013. Why mechanisms shouldn't be ignored-commentary on Nettle by Brown. Behav Ecol. 34:1041–1042.
Nettle D, Gibson MA, Lawson DW, Sear R. 2013. Human behavioral ecology: current research and future prospects. Behav Ecol. 34:1031–1040.
West SA, Burton-Chellow MN 2013. Human behavioral ecology. Behav Ecol. 34:1043–1045.