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The pleasures and pitfalls of studying humans from a behavioral ecological perspective

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We know it's incredibly tedious, but we have to admit we agree with everything [Nettle et al. \(2013\)](#) say. Not only is that tedious, it also makes for a rather brief commentary. So, in an effort to keep the conversation lively, we would like to address some additional issues that highlight the pleasures and pitfalls of studying humans from a behavioral ecological perspective. Before we begin in earnest, we think it is perhaps worth drawing a distinction between the contribution made by human behavioral ecology (HBE) to the broader field of behavioral ecology (BE) versus the contribution that BE makes to the study of humans from an evolutionary perspective. We think this is a distinction worth making as [Nettle et al. \(2013\)](#) interpret the low number of papers published in flagship BE journals as a signal of a (potentially increasing) risk of isolation from the broader field; something they suggest can be traced, at least partly, to the "disco problem" as defined by [West et al. \(2011\)](#). Although this may well be true, it is also

worth considering whether these numbers are, in fact, roughly what we'd expect for such a large, long-lived mammal (other long-lived species like elephants and chimpanzees are similarly underrepresented compared with birds, fish, and insects). We are, after all, a terrible species in which to address fundamental evolutionary questions, not only because of our long life spans and slow rates of reproduction but also because of the obvious ethical constraints placed on experimental studies of human behavior. It is a rather sobering conclusion, but if we take a broader, less anthropocentric view, it may be that we cannot, or rather should not, expect HBE to make major theoretical or empirical contributions to BE, which can apply to the field as a whole. This shouldn't be confused, of course, with our saying that it is not worthwhile to study humans or indeed other long-lived mammals (we'd both be out of a job for a start, if this were the case).

THE DISCO PROBLEM REVISITED

All is not doom and gloom, then. It is clear that BE offers an excellent framework for the study of human behavior. The combination of methodological rigor and well-developed evolutionary theories serves extremely well as a guide to human studies. As [Nettle et al. \(2013\)](#) point out, the contribution that BE has made, and continues to make, to the study of humans in their natural social settings is impressive. Yet, the trick when applying ideas originally from the animal literature to human behavior is to ensure that the right kinds of comparisons are made in the right kinds of ways.

More specifically, we should try to avoid using terms from the animal literature to describe human behaviors when they represent nothing more than loose illustrative metaphors rather than attempts to apply theory in a rigorous and truly comparative fashion. There are, for example, studies that refer to human "lekking displays," where certain aspects of male behavior in social settings are argued to be specifically aimed at mate attraction (e.g., [Lycett and Dunbar 2000](#); [Braithwaite 2008](#)), and at least 1 study has drawn parallels between leks and human behavior in nightclubs ([Hendrie et al. 2009](#)). None have gone so far as to claim that actual mating takes place on the dance floor, and also most researchers would not suggest that human females seek only gametes from their mates; yet both of these are key characteristics of lek mating systems ([Wiley 1991](#)). In other words, although these metaphors seem to be an appealing means of bridging the gap between humans and other animals, they may simply confuse the issue, and the extent to which such comparisons illuminate our understanding of human mating systems is limited. This more literal form of the disco problem may stem at least partly from a tendency to cherry-pick the animal literature to find a relevant comparison. Given the immense diversity of species, it is always possible to find a bat, bird, or bug that shows a behavioral pattern ostensibly similar to humans as a means to prove a point but, again, the value of such comparisons is often questionable. This problem will obviously diminish as we gain even more detailed knowledge of human systems (and, as such, we are reinforcing [Nettle et al.'s \(2013\)](#) point with regard to encouraging more HBE studies); cherry-picking will become less likely as we characterize the scope and limits of the human niche in more detail, and our use of BE models and species comparisons will become increasingly more sophisticated as a result. As [Nettle et al. \(2013\)](#) note, an increased methodological sophistication can already be seen in the use of large demographic and social survey databases to answer core behavioral ecological questions. The relationships observed in such data, however, often explain only a small proportion of the variance. Although it is clear that such small effects hold biological significance, it is equally clear that, to obtain a fully satisfactory explanation of these phenomena, we need more

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.

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Received 17 December 2012; accepted 27 December 2012.

doi: 10.1093/beheco/ars231

Advance Access publication 22 January 2013

Forum editor: Sue Healy

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

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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