What HBE is forgetting is that cultural transmission ultimately has the potential to generate distinct evolutionary pathways through the creation of nonrandom sources of variation (Jablonka and Lamb 2005). This is because evolved learning biases (such as copying from the most frequent or the most prestigious model) allow traits to spread in ways that are not necessarily fitness enhancing for the bearer. The fact that conformist transmission can allow for cultural group selection (Henrich and Boyd 1998; Bowles and Gintis 2011) demonstrates quite palpably that human researchers cannot safely relegate cultural transmission to the black box of a phenotypic gambit (Laland et al. 2011). Although there is plenty of room for debate (see e.g., Dickins and Rahman 2012) over whether or not conventional organic natural selection can or cannot override the influence of alternative sources of selection (such as cultural transmission), the very fact that this is not resolved suggests to me that HBE should be paying more attention to how individuals acquire information. The exclusion from this review of longitudinal behavioral ecological analyses afforded by the archaeological record (e.g., Kennett and Winterhalder 2006) accentuates this problem.

This is not a critique of this excellent review, only a reminder of how we need now to look more closely at how individuals acquire traits, because "how" questions may help to explain "why" questions.

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Human behavioral ecology

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Nettle et al. (2013) have done an excellent job of showing what an exciting time it is for the field of human behavioral ecology (HBE). Research is tackling an increasing range of fundamental problems at the interface of several biological and social science disciplines. Here, our aim is to raise general issues, influenced by our experience of the literature on cooperation in humans (West et al., 2011). Specifically, 1) social learning and cultural evolution can make it harder to make unambiguous predictions with humans; 2) the study of humans presents a number of methodological challenges; and 3) whether any aspects of human behaviour are special is an empirical question, and not just something that can be asumed.

FITNESS AND CULTURE

The success of the behavioral ecology approach is built on an extremely solid theoretical grounding (Davies et al. 2012). Darwin (1859) argued that traits that increase fitness will accumulate in populations, leading to organisms that behave as if they are trying to maximize their fitness. Our modern most general genetical interpretation of this is that organisms should behave as if they are trying to maximize their inclusive fitness (Hamilton 1964; Grafen 2006). The beauty of this is that it takes evolutionary theory based on gene dynamics and translates it into a theory about how individuals should behave in a way that is highly amenable to empirical testing.

Although this approach is no doubt also central to HBE, cultural evolution can make things more fuzzy because it can favor traits that don't maximize genetical inclusive fitness. Genetical evolution will have favored social learning mechanisms that increase genetical fitness (Boyd and Richerson 1985). However, we now live in environments that are different to those in which these learning mechanisms evolved, and so there is the potential for social learning mechanisms to lead to cultural evolution in any direction, increasing or decreasing fitness. We might expect genetical evolution to respond to this and bring social learning back into line with inclusive fitness interests. In practice, we shouldn't expect this to have happened, because cultural and genetical evolution can occur over very different time scales, there has only been a relatively short time for genetical evolution to respond, and modern human populations can have low genetical selection pressures/coefficients.

The problem here is that we should not expect clear unambiguous predictions from cultural evolution, analogous to that of inclusive fitness maximization that arises from genetical evolution. This is because details matter, such as the mechanisms of social learning, how transmission occurs, and the nature of the trait, all of which vary across cultural traits. Cultural evolution is, therefore, perhaps more analogous to epidemiological processes than genetical selection. To give a specific example of how much details can matter, considering almost identical models for the evolution of cooperation, different researchers have come to completely opposite predictions that cultural selection leads to either greater or lower levels of cooperation than genetical selection (Boyd and Richerson 2002; Boyd et al. 2003; Lehmann et al. 2007, 2008; Lehmann and Feldman 2008).

Determining whether any and what kind of generalizations can be made about cultural evolution remains one of the greatest problems for HBE. Even some of the most basic theoretical questions remain to be answered, let alone empirically tested. Are any generalizations possible, or do we need to examine each situation on a case-by-case basis? Will culture be more important for certain classes of traits, such as those less linked to fitness?

TESTABILITY

The experimental manipulations that are carried out on nonhuman animals are often not possible to the same extent with humans. For

example, it is relatively easy to manipulate the number and sex of offspring that a bird is caring for (Davies et al. 2012), but less so with humans. This has at least three consequences for work on humans.

First, there is a greater focus on tackling behavior in humans from a mechanistic perspective. In many cases, this has led to confusion between ultimate and proximate explanations (Scott-Phillips et al. 2011; West et al. 2011). For example, results showing that "it feels nice" or "the brain rewards punishing behaviors" are not answers to the evolutionary problem of cooperation. Furthermore, in some cases, confusion between proximate and ultimate factors has led to an overinterpretation of proximate patterns. For example, there are multiple explanations for why humans might cooperate in public goods games, and it shouldn't just be assumed that a novel evolutionary force is required (Kümmerli et al. 2010; Burton-Chellew and West 2013). Such problems are best solved by exporting experimental design and interpretation procedures that are standard in nonhuman research into human research, such as the proper controls, the testing of a priori predictions, and experiments that allow hypotheses to be falsified (Parker and Maynard Smith 1990; Kümmerli et al. 2010; Davies et al. 2012; Burton-Chellew and West 2013).

Second, as with behavioral ecology more generally, the best research combines different methodological approaches. HBE researchers have shown great ingenuity in advancing the methodologies for carrying out observational, experimental, and comparative work, in both laboratory and "field" scenarios. For example, economic games in labs (Falk and Heckman 2009), field experiments where participants don't even know they are in an experiment (Bateson et al. 2006), observational field data (Ernest-Jones et al. 2010), TV game shows (Burton-Chellew and West 2012), cross-cultural comparative studies (Currie et al. 2010), and the same economic game played in different cultures/environments (Henrich et al. 2005; Lamba and Mace 2011). Each of these methodologies has its own pros and cons, and progress will be best made by combining them, rather than arguing which is best, as demonstrated by work on nonhuman animals (Davies et al. 2012).

Third, work on humans offers certain challenges to the optimality approach. One issue, touched on above, is that humans are probably experiencing a considerable evolutionary lag with their environment. Another issue is the extent to which humans rationally alter their own behavior in accordance with their wants and desires (although of course these wants and desires are mostly the result of selection pressures themselves). These issues can make conclusions based on optimal responses somewhat difficult, especially when optimality is measured through proxies such as economic success rather than actual fitness. For example, studies of inheritance patterns and parental allocation of offspring would appear to support an adaptationist stance (Boone 1986; Bereczkei and Dunbar 1997; Hill 1999; Deady et al. 2006), but could also result from good economic practice. Consequently, HBE can be at its most illuminating when it can show adaptive behavior that is either the result of nonconscious processes or is contra to the prediction of other approaches. For example, sex ratios at birth, cues that influence cooperation, or attitudes toward third-party recreational drugs (Lummaa et al. 1998; Bateson et al. 2006; Kurzban et al. 2010).

SPECIAL

To conclude, one of Nettle's et al. (2013) main points is that HBE rejects "the notion that fundamentally different explanatory approaches are necessary for the study of human behavior as opposed to that of any other animal." This contrasts with many studies of humans, where the starting assumption is that humans are special and that special explanations are required. Although there is no doubt that there could be unique things about humans, such as a significantly greater potential for cultural evolution, uniqueness is something that needs to be empirically demonstrated, rather than just assumed. To give an extreme example, although it has been claimed that "human altruism goes far beyond that which has been observed in the animal world" (Fehr and Fischbacher 2003), humans are actually far less altruistic than a huge range of organisms, including bacteria, slime molds, and ants (West et al. 2011). This emphasizes that one of the beauties of the behavioral ecology approach is that it provides a unified framework for comparing and contrasting the behavior of all living organisms.

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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