and even stated offspring sex preferences of higher-status Maasai. Their difficulties in convincing anyone that they are real Maasai makes sense in light of signaling theory. Signals, including ones about ethnicity, are believable only if there is some guarantee of their truthfulness. One way to provide such a guarantee is to make a signal difficult to fake, and ethnic signals generally have that quality. Mukogodo awareness of this is shown by the fact that they chose to emulate the Maasai, who were removed from the area by the British in the early twentieth century, rather than the remaining high-status Maa speakers in the region, the Samburu. Whereas no Maasai were left to challenge Mukogodo claims to Maasai identity, any claims to Samburu identity could easily have been dismissed by the Samburu themselves. Other applications of signaling theory to human affairs include studies of fishing (Sosis 2000), hunting (Bliege Bird et al. 2001), dancing (Brown et al. 2005), cosmetics (Cronk et al. 2002), engagement rings (Cronk & Dunham 2003), political rhetoric (Johnson 1986; 1987; 1989; Salmon 1998), kin terms (Chagnon 1988; 2000), religion (Cronk 1994; Irons 1996; Sosis & Alcorta 2003), and interpersonal communication (Gerkey & Cronk 2005).

Signaling, which generally occurs at very short timescales, clearly belongs in the category of microevolutionary processes. The question arises, therefore, of how to relate it to other microevolutionary process and to cultural macroevolution. One approach to this problem is to emphasize the aspects of signaling theory that focus on receiver psychology (Guilford & Dawkins 1991). The basic idea is simple: Signals, whether they are designed by natural selection or by advertising executives, should be designed to fit the psychology of the intended receiver. Similarly, cultural traits may be more successful in persisting in the minds of individuals and in being replicated if they are memorable and attention-grabbing (e.g., Boyer 1994 on religious concepts). In this way, evolved human psychology becomes the link between the short life of an individual signal and the long life of a cultural tradition, and intentionality can be given the role it deserves in the unified science of cultural evolution outlined by Mesoudi et al.

A continuum of mindfulness

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Abstract: Mesoudi et al. overlook an illuminating parallel between cultural and biological evolution, namely, the existence in each realm of a continuum from intelligent, *mindful* evolution through to oblivious, *mindless* evolution. In addition, they underplay the independence of cultural fitness from biological fitness. The assumption that successful cultural traits enhance genetic fitness must be sidelined, as must the assumption that such traits will at least be considered worth having.

Mesoudi et al. provide a valuable survey of the parallels between biological and cultural evolution, but they ignore or underestimate several other parallels that go some way to explaining the intensity of the distaste with which many researchers in the humanities and social sciences view *any* attempt to introduce Darwinian thinking into their domains. When Darwin first proposed sexual selection as a significant factor in biological evolution, it was greeted with both dismay and delight: To some it was an ominous backslide from the mindless purity of natural selection, whereas to others it was a welcome relief, restoring cherished elements of "mind" into evolution (Cronin 1991; Dennett 1995). But Darwin had already shown us the continuum from foresighted attempts to redesign nature through to utter mindlessness in his trio of *methodological* selection (in deliberate breeding and crossing), *unconscious* selection (in early domestication – which we might call domestication *without intent*), and *natural* selection proper, which invokes no minds or cognitive discriminations at all. It is important to avoid the common misconstrual that views methodical and unconscious selection as *alternatives* to natural selection, rather than as special *varieties* of natural selection, in which the selection pressure is focused through events in the nervous systems of the domesticating species. There is nothing counter-Darwinian, of course, in either phenomenon; intelligence *did* evolve by natural selection "proper" and thereupon became a potent selective force in the environment. Early domestication was thus an interspecific variation on sexual selection, in which the (cognitive) eye of the selector plays a crucial – but, of course, non-miraculous – role (Miller 2000). Neither the choosy females nor the early keepers of animals needed to understand their role in the "improvement of the breed." To these selective phenomena we can add the more recent and still more mind-requiring tinkerings of genetic engineering. The processes of generate-and-test that yield the would-be replicators come in all varieties of intelligence, but in the end, as Crick reminds us, Orgel's Second Rule applies: Evolution is cleverer than you are (Dennett 1995).

What many thinkers in the humanities and social sciences find abhorrent in evolutionary perspectives is the imagined implication that any such model will replace the traditional freedom of will, rational authorship, and artistic genius imputed in their disciplines with mindless random mutation and mechanical selection. And indeed, in cultural evolution, as Mesoudi et al. make abundantly clear, there are undeniable cases of cultural features that evolve by Darwinian processes without any need to invoke authors, designers, or other intelligent creators. Most obviously, languages – words and pronunciations and grammatical features – evolve without any *need* for grammarians, deliberate coiners, or other foresighted guardians of these cultural items. But what Mesoudi et al. never properly acknowledge is that the traditional perspective of the humanities, in which intelligent authorship, foresighted, purposeful reasoning, and artistic judgment occupy center stage, also has a place in the evolutionary picture, so the dread of the humanists is misplaced. Again, there is a continuum, with many different levels of mindfulness or rational engagement to be discerned. There is unconscious selection (as Darwin would say) of musical styles, for instance, methodical selection (with much planning and debate) of political arrangements and elements of religious dogma, for example, and attempts at *memetic* engineering by advertisers and even scientists seeking the best – most vivid and unforgettable – acronym for their novel theory or investigative method. And here, as before, Orgel's Second Rule applies. No matter how intelligent, foresighted, and purposeful the local process may be, most of the brainchildren of human cultural vectors fail to found long-lived lineages.

Another point that is underplayed in the target article is the extent to which cultural traits can flourish or perish independently of their effects on our genetic fitness. Because cultural evolution can occur in orders of magnitude faster than genetic evolution, many of its prominent patterns must be stabilized by forces that are only weakly related, at best, to the reproductive success of their vectors. The default presumption that all cultural traits that do evolve will be fitness-enhancing needs to be firmly set aside. Mesoudi et al. are right that this assumption is not uniformly made, but it is often tacitly implied or suggested by the way people write about cultural evolution. For example, the fact that some form of religion is found in every human group that has ever been studied leads many to conclude that religion *must* be enhancing to either individual or group fitness, but this is a serious non sequitur; the common cold also is found wherever there are people, but presumably it is not fitness-enhancing at all. It has evolved because it could evolve.

One may, of course, treat these shifting features of human culture as mere "noisy" variation around the few cultural traits

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that do have a clear and measurable positive impact on genetic fitness, but this squanders the opportunity to see them as having their own fitness, as symbionts competing for rehearsal space and for opportunities to leap from host to host. The arms races that are conducted within each of us between our immune systems and our pathogens are themselves evolutionary phenomena, on a fast timescale, and they, too, have their parallels in cultural evolution. We certainly do not evaluate our ideas on the basis of their contribution to our *genetic fitness* – most of us do not care much about that goal – and the standards we *do* adopt are themselves products of cultural evolution. Even the presumption that any cultural item that spreads widely will at least be *deemed* (rightly or wrongly) to be worth having must be set aside, as it may instead be an unappreciated or even detested item that is just too well entrenched for the local coalition of cultural antibodies to remove. Advertising jingles are good examples.

We are largely in agreement with Mesoudi et al. about the parallels they describe, but think they have overlooked these further points that may prove equally fruitful in the project of studying culture with a unifying evolutionary framework.

Evolution is important but it is not simple: Defining cultural traits and incorporating complex evolutionary theory

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Abstract: Examining homology in biological and cultural evolution is of great importance in investigations of humanity. The proposal presented in the target article retains substantial methodological weaknesses in the identification and use of "cultural traits." However, with refined toolkits and the incorporation of recent advances in evolutionary theory, this overall endeavor can result in substantial payoffs for biological and social scientists.

Mesoudi et al. present the premise that human culture undergoes Darwinian evolution and that key aspects of biological evolutionary patterns can be applied to the understanding of cultural change. The goal of this article is to promote a "more progressive and rigorous science of culture" (sect. 1, para. 3). However, as with the majority of treatments of this topic (cf. Richerson & Boyd 2005), the authors rely too heavily on psychological and linguistic examples. They do not attempt incorporation of a wide range of ethnographic data sets (the most overt nod to ethnography is a few paragraphs in sections 2.3.2 and 3.3.2) and they focus on uses of "culture" and "cultural traits" that most anthropologists will find problematic. Here I critique this key area and suggest a few additional evolutionary perspectives that could be useful in this project.

Simplifying assumptions have become a mainstay in biological theorizing. The immense complexity in genomic, developmental, and other biological systems has led to the use of simple models to create baseline parameters for assessing the mechanisms of said systems. Cultural systems, however, may not be as homologous to biological ones as is assumed by the authors of this article. They assert that one can overcome Galton's problem by treating "cultural traits" as equivalent to biological characters. They also suggest that because vagaries in biological units (such as "gene") do not inhibit the use of evolutionary models, the relatively vague "cultural trait" units are also amenable to similar applications (see sect/2.1). They state that the "apparent lack of discrete particles in culture equivalent to genes" (sect. 3.5.2) is not an inhibitor to the use of basic Darwinian models for cultural change. The authors do address the contention that there may be substantial differences between patterns of biological and cultural change (see sect. 4), but do not incorporate these perspectives into their analyses of mechanisms in any central manner (sects. 2 and 3).

The authors use the term "cultural trait" at least 27 times without offering an explicit definition. In section 2.1.2 they suggest that cultural traits are things such as "language, tools, customs, or beliefs." Of the many cultural traits mentioned in the article, the majority used in concrete examples supporting homology with biological systems are aspects of language or results from tests conducted by English-speaking experimental psychologists and economists. Others include patents, guns, teddy bears, stone tools, kinship patterns, behavioral rules, dairy farming, justice, money, the electric motor, the QWERTY keyboard, and religious beliefs, for example. A significant problem with this use of "cultural trait" is the lumping together of diverse elements that may not share common structural components or patterns of heritability.

If we are interested in modeling selection on cultural traits, we can look to two levels: phenotypic interactions with environments and other phenotypes, and trait-trait competition. That is, traits do not exist in a vacuum (biological or cultural), and therefore understanding of the phenotype (or the phenogenotype for biocultural contexts, sect. 3.1.2) in which they participate is core to modeling an evolutionary system. Alternatively, one can ignore the complexity at the phenotypic level and model trait-trait competition (usually seen as allelic competition in biology). However, any competition model must utilize similar "competing" units. Although section 3 of the article goes to great lengths to suggest that cultural and biological patterns of inheritance and change are roughly equivalent, the examples Mesoudi et al. provide often do not form compatible units for comparison. Psychological and economic experiments using two-choice option models may not be equivalent units to multiple chain event transmission sequences (sect. 3.2.2). Transmission of how to behave at a restaurant (a highly culturally contextual "unit") may not break down into the same units as anagram-solving choice tests.

The biological examples provided in section 3 use overt behavioral and physiological measurements or assessments, whereas most psychological and anthropological research relies on perceptions, semantic exchanges, and culturally contingent decision processes. Measuring the constituent "traits" in cultural phenotypes can be a very different process with distinct results compared to biological systems and traits (however they are defined). A significant contribution to this endeavor would be the creation of specific definitions and measurement tools that can effectively represent diverse types of cultural patterns and elements. By moving these inquiries beyond an over-reliance on the most easily quantifiable cultural elements, such as those emerging from many language studies, we could achieve a more accurate comparison between systems of biological and cultural change.

It is possible that the landscape (environment or ecology) in which culture exists and changes may not be best, or primarily, amenable to modeling by standard neo-Darwinian approaches. However, recent enhancements of Darwinian perspectives such as developmental systems theory (Oyama et al. 2001) and niche construction theory (Odling-Smee et al. 2003) may offer more appropriate tools for the synthesis that Mesoudi et al. are proposing. Kevin Laland, an author of the target article, is also one of the major proponents of niche construction theory. I am surprised at the relative absence in the target article of this important addition to modern evolutionary perspectives. I suggest (echoing Odling-Smee et al. 2003) that niche construction may be a highly appropriate model for understanding patterns of human change. It may also be that developmental systems theory, with its emphasis on joint determination by multiple causes, extended inheritance, context sensitivity and contingency, and development as construction (Oyama et al. 2001), provides a more complex and contingent, but ultimately more satisfying, model for understanding homologies between

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