The Evolutionary Culture Concepts

Catherine Driscoll*

Most attempts to define culture as used in the cultural evolution literature treat culture as a single phenomenon that can be given a single nondisjunctive definition. In this article I argue that, really, cultural evolutionists employ a variety of distinct but closely related concepts of culture. I show how the main prominent attempts to define a culture concept fail to properly capture all the uses of "culture" employed in cultural evolutionary work. I offer a description of some of the most important culture concepts used by cultural evolutionists.

1. Introduction. This article is intended to argue that there are actually multiple concepts of culture used in the cultural evolutionary sciences. The cultural evolutionary sciences are a relatively newly emerging field that seeks to understand how culture evolved as a trait or set of traits in human evolutionary history and how cultural traits evolve by social learning processes in human populations; they also connect human and animal cultural capacities. The subfields include dual inheritance theory (Boyd and Richerson 1985; Mesoudi 2011), gene culture coevolution (Feldman and Laland 1996; Laland, Odling-Smee, and Feldman 2000), the "epidemiology of representations" theorists (EoR; Sperber 1996; Atran 2001), parts of evolutionary behavioral economics (Bowles and Gintis 2011), and, to a lesser extent, memetics (Blackmore 1999; Dawkins 1999).

This article is not intended to be a general analysis of the content of the culture concept used in all the various social and biological sciences that employ the term: this would be too big a topic for a single article. Moreover, there are differences in the methodology and explanatory approaches to culture between cultural evolutionary sciences and the social sciences, especially social sciences such as cultural anthropology, sociology, and history,

Received September 2015; revised January 2016.

*To contact the author, please write to: Department of Philosophy and Religious Studies, North Carolina State University, Raleigh, NC 27695; e-mail: catherine_driscoll@ncsu.edu.

Philosophy of Science, 84 (January 2017) pp. 35–55. 0031-8248/2017/8401-0003$10.00
Copyright 2017 by the Philosophy of Science Association. All rights reserved.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

that suggest that the concept is being used in an importantly different way in the cultural evolutionary sciences (Fracchia and Lewontin 1999; Ingold 2007). This is coupled with a degree of coherence within the cultural evolutionary sciences that suggests they share a common body of research questions, theory, methods, and models; they also have a type of critical dialogue between subfields that suggests their work is sufficiently commensurable to share a common culture concept or concepts (for a discussion, see Laland and Brown 2002; Mesoudi, Whiten, and Laland 2006). So while there are relationships between the cultural evolution and social science concepts of culture (certainly they are historically related, and certain cultural evolutionists such as Mesoudi et al. [2006] intend to connect their concept of culture with the social science concepts), it is not unreasonable to isolate the culture concept of the cultural evolutionary sciences in this article.

My argument in this article is as follows. First, the term "culture" is employed by the cultural evolutionary scientists in a variety of very different ways in different parts of their work. It is possible that either these different uses really represent different culture concepts or possibly, as many cultural evolutionary scientists and others seem to think, there is some single definition of culture that can capture them all.[1] Consequently, a number of such culture concepts have been proposed in the cultural evolution literature, for example, the view that culture is information acquired by social learning (see, e.g., Richerson and Boyd 2005) or that culture is a system of behavior and its products (e.g., Jablonka and Lamb 2005). However, the current single definitions of culture offered in the literature cannot capture all of the different ways the term is used. The different culture concepts also do not simply represent uses in different cultural evolutionary science subfields: instead, they seem to refer to different levels or parts of cultural evolutionary phenomena. I conclude that the different uses of "culture" are explained by there really being a family of distinct culture concepts that share a variety of different features and connections between them.[2]

I therefore proceed as follows: section 2 describes the various ways in which the culture concept is used in the cultural evolution literature. In section 3 I discuss how far the definitions of culture offered in the literature can capture these uses: I argue that none of them alone is sufficient to capture the range of uses to which the culture concept is put. Section 4 offers some de-

1. One exception to this general view of the culture concept may be Lewens (2015), who also notices some of the variety of culture concepts actually used by cultural evolutionary scientists.

2. One possibility, therefore, is that the evolutionary concept of culture in general might be best understood as a prototype, as has been proposed to be the case for the gene concept (Stotz and Griffiths 2004). While this goes a bit beyond the scope of this article, I discuss this possibility briefly in the conclusion.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

scriptions of what I think are the multiple culture concepts being used in the cultural evolutionary sciences.

2. The Uses of the Culture Concept in the Cultural Evolutionary Sciences. The first order of business, then, is to consider the range of different ways the culture concept is used in the cultural evolutionary sciences. I will consider five different types of work: work in humans, work in nonhuman animals, niche construction models, group-level models, and explanations of the origin of culture.

2.1. Individual-Level Explanations of Human Culture. The commonest of all types of cultural evolutionary explanation are those focused on individual-level human culture. Cultural evolutionary work is called evolutionary for multiple reasons. The primary reason is its focus on understanding how culture is transmitted and evolves in various types of human populations. Culture is understood as the effect or output of a biological adaptation (also sometimes treated as "culture"; I will come back to this shortly), a capacity that has the function of permitting humans to acquire phenotypic traits that on the whole raise their fitness without having to go through the lengthy process of ordinary natural selection (Boyd and Richerson 1996). One consequence of this is that individual-level models treat culture at once as something primarily possessed by *individual* humans as "information . . . capable of affecting [their] behavior" (Richerson and Boyd 2005, 5) and something that takes the form it does because those humans nonetheless live in a particular kind of social environment or population in which particular kinds of cultural evolutionary processes occur (Boyd and Richerson 1985). Another consequence is that researchers in these various fields describe culture as, or in terms of, certain phenotypic traits of individuals. Occasionally (mostly in informal explanations) individual-level culture is described as a series of psychological traits: consider, for example, the values of the Pennsylvania family farmers described by Richerson and Boyd (2005), the preferences for seeing free riders punished on the behavioral economists' explanations of strong reciprocity (Bowles and Gintis 2011), or the mental representations in Sperber's (1996) explanations of reconstruction. Formal models, however, often describe the transmission of *behaviors* or patterns of behavior, for example, punishment (Henrich and Boyd 2001b) or farming (Aoki, Shida, and Shigesada 1996); even Sperber, writing with a colleague, does this on one simple model of the transmission of smoking behavior (Claidiere and Sperber 2007). In some cases, the models or explanations instead describe the evolution of an *artifact* (such as a kayak or spear): this is obviously common among paleoanthropologists (e.g., Lycett and von Cramon-Taubadel 2008; Eren, Buchanan, and O'Brien 2015) but also occurs in the standard cultural

https://doi.org/10.1086/688934 Published online by Cambridge University Press

evolution literature in which the case being considered requires using paleoanthropological data (see, e.g., Henrich 2004).

The (on the whole) adaptiveness of human culture is proposed to be primarily due to the nature of social learning. Social learning in the simplest sense means something like "learning from others" rather than "learning by oneself." However, social learning can involve any degree of social mediation of learning from detailed, high fidelity imitation all the way to forms of learning common in animals (such as goal emulation or stimulus enhancement) whereby environments are constructed by conspecifics in such a way that trial-and-error individual learning by individuals reliably leads to their acquisition of the appropriate trait (Whiten 2000; Heyes 2012). Different social learning methods result in different cultural evolutionary processes (Henrich and Boyd 2001a; Henrich and Gil-White 2001). All social learning of any type, however, involves exploiting the social environment and the similarities between self and others to potentially reduce the costs of learning (Aoki and Feldman 2013); given complex, cumulative evolution, individuals can thereby acquire much more adaptive behaviors than they could alone (Boyd and Richerson 1996). While cultural evolutionists such as the dual inheritance theorists and EoR researchers disagree on what goes into the social learning process in humans—that is, imitative learning for the dual inheritance theorists (Boyd and Richerson 1985) and something close to reconstruction of a trait from impoverished evidence for the EoR group (Sperber 2000)—both nevertheless accept that social learning is the core feature of cultural transmission.

Finally, perhaps the feature of culture on these models that makes them genuinely evolutionary is that the consequence of social learning is that a successful cultural trait (whether it be a behavior, artifact, or mental representation) is *repeatedly* copied or reconstructed (although not necessarily very precisely—more on this later) such that, generally, tokens of the same type of trait form a lineage or set of lineages in a population.[3] Processes of cultural evolution can then generally lead to the differential creation or survival of lineages in a population via a variety of different cultural processes (Boyd and Richerson 1985).

2.2. Individual-Level Explanations of Animal Culture. Another type of phenomenon on which cultural models focus is individual-level culture

3. Unlike other authors, I focus on lineage formation here in the sense of a set of cultural traits *connected causally by social learning*—or perhaps by a flow of information—rather than in the sense of reproduction or replication. This is to respect Sperber's (2000) concerns about the role of reconstruction in social learning and because high fidelity replication is not necessary to cultural evolution. There are a few cultural evolutionary models that rely on replicating population averages rather than having very distinct competing lineages (Henrich and Boyd 2002), but these tend to be very exceptional cases.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

as found in nonhuman animals, especially close relatives of humans such as chimpanzees. The animal culture described in these models is primarily also composed of individual-level, socially learned, phenotypic traits that form lineages and spread through populations. For example, Whiten and colleagues identify 65 behavior patterns that appear to be present in a variety of chimpanzee groups (2001). However, nonhuman animal culture also has some significant differences from the parallel phenomenon in humans. For one, chimpanzee culture relies more than human culture on socially facilitated trial-and-error learning such as *goal emulation* or *stimulus enhancement*. Both types of cases require the chimpanzees to engage in significant learning on their own in order to acquire the appropriate behavior (Whiten 2000).

While nonhuman animal culture is of significant interest in its own right, a major reason for pursuing this work is to understand the relationships between human and nonhuman animal culture (Whiten 2000; Laland and Hoppitt 2003). Chimpanzee culture, for example, as a capacity, is often treated as a potential homolog of human culture, and culture in less closely related animals as an analog of human culture (Galef 1992). In this sense then, "individual-level culture" in these types of explanations is taken to refer to something that both chimpanzees and humans can have in common, and this is not just the presence of individual-level socially transmitted phenotypic states but possibly some of the competences that underlie them (I return to this shortly).

2.3. Niche Construction Models. Another phenomenon on which cultural evolutionary models have focused is the phenomenon of *niche construction*, the idea that animals can modify the selection pressures acting on them and their lineage by modifying the environment and then transmitting that modified environment to their offspring or members of the next generation in their population or group. While these models are primarily aimed at understanding how the transmission of environments can modify the transmission of genes, similar effects can occur with cultural traits, and the cultural evolutionists have developed corresponding cultural evolutionary and gene-culture niche construction models (Laland, Odling-Smee, and Feldman 2001; Odling-Smee, Laland, and Feldman 2003). Even in some fairly classic gene-culture models, the "culture" is also partly composed by the environment; for example, in the famous sickle cell case, it is agricultural changes to the environment that led to mosquito proliferation and the changes in the distribution of genes for sickle cell anemia (Feldman and Laland 1996). These models lead to a relatively natural understanding of these modified environments as culture in themselves. For example, Odling-Smee and Laland, taking a "broad understanding of culture," argue that "cultural inheritance does not comprise only the transmission of brain-based knowledge

https://doi.org/10.1086/688934 Published online by Cambridge University Press

through teaching and social learning. . . . Generations of humans also inherit culturally modified rural and urban environments—fields of crops, terraces, artificial lakes, canals, roads, schools, hospitals, factories, police forces, electricity grids, waste products, and pollution" (2011, 227). Similarly, Richerson and Boyd, for example, accept that the information they think comprises culture can be in environmental changes and in artifacts (2005, 61).

However, this "culture as modified environment" is not just a simple "extended phenotype" caused by the mental states and behaviors making up ordinary individual-level culture. It can be the consequence of group behavior, it can persist and affect the fitness of future generations, and it is not always replicated. What is more, a variety of authors accept that modified environments also act as part of the social learning system in their own right: for example, Richerson and Boyd (2005) and Odling-Smee and Laland (2011), among others, agree that part of the information that permits social learning can be stored in the environment.

2.4. Group-Level Explanations of Human Culture. A fourth type of work in the cultural evolution literature treats culture as a phenomenon that also occurs at the group level. There are a variety of slightly different types of group-level culture, but the upshot of all of these is that it is possible for groups to possess group-level cultural traits that have an evolutionary history in their own right.

All group selection models, cultural or genetic, involve an interaction between two evolutionary forces: a selective force acting on group-level traits and a selective force acting on individual-level traits; most commonly in group selection models the group-level trait is simply some aggregate of the traits of the individuals making up the group (e.g., the proportion of altruists making up a group). The forces acting on the group-level traits (e.g., the fitness effects of there being a high proportion of altruists in the group) then interact with the forces acting on the individual-level traits (e.g., the fitness effects of being a nonaltruist within that group) to determine the fate of the whole group (Sober and Wilson 1998). The fitness effects of these forces can then be felt at the level of the individual (in the group [and individual] selection process called "Multi-level Selection 1," or MLS1) or at the level of the group (in the group [and individual] selection process called "Multi-level Selection 2," or MLS2). This means that the consequence of positive group selection is either an increase in the number of individuals making up the group (MLS1) or (in MLS2) that the group itself splits and produces more groups (Okasha 2006). Such processes are generally referred to as "*cultural* group selection" when the group-level traits are composed of traits that are socially transmitted (rather than genetically heritable) at the individual level. Cultural group selection can take similar forms with models that are both effectively MLS1 (Henrich and Boyd 1998) and MLS2

https://doi.org/10.1086/688934 Published online by Cambridge University Press

(Soltis, Boyd, and Richerson 1995; Bowles 2006). However, either way, the group-level cultural trait is taken by these models to have an effect and a cultural evolutionary history in its own right, which interacts with and even against the effect of the individual-level traits in the same group.

To make this more obvious, consider multilevel selection explanations that are not simply aggregative but in which there are coherent, functional, group-level behaviors or traits of whole groups and organizations that are composed of potentially highly various contributions from their members. One obvious example is from Wilson's (2002) work on the (cultural) evolution of religion, which sees religion as a cultural group-level adaptation for constituting individuals into an *organization* that can drive adaptive collective action and promote group or individual fitness. Many religious groups, businesses, and other organizational activities are made up of interacting human parts: consider a religious ritual in which different members perform different behaviors possibly using different artifacts or constructed environments. In these sorts of cases the functional effects of these group-level traits do not come just from the particular contribution of any individual-level trait but from their interaction in a group-level whole.

Another plausible "group-level" cultural phenomenon is found in work on cultural phylogenies. Cultural phylogenetics examines large-scale *traditions* in individual-level cultural traits. Traditions are "bundles" of lineages of similar, usually related, individual-level cultural traits within a group; as such they constitute group-level cultural phenomena. Traditions can vary over time and between groups because of the nature of the lineages composing them; cultural phylogenetics seeks to determine the relationships between similar traditions in different groups, in particular whether they are formed by phylogenetic branching or assimilation, by examining patterns of differences and similarities between those traditions (Jordan and Shennan 2003; Matthews et al. 2011). The nature of such traditions can be used to determine relationships between the groups that use them and have also been applied to nonhuman animal cultural traditions (Lycett, Collard, and McGrew 2009).

Work on cultural group selection and phylogenetics, therefore, also seems to use another type of culture concept, a concept of group culture, which, while composed of individual-level culture, nevertheless warrants its own set of cultural evolutionary models and explanations. Cultural evolutionists do not often explicitly call these various group-level cultural phenomena "group-level culture," although they come pretty close, for example, describing group-level "cultures" that have such evolutionary effects (Bowles and Gintis 2011, 16, 33) or "cultural variation . . . at the level of groups" in group-level traits such as "solidarity" (Richerson and Boyd 2005, 14) or "cultural information" in the form of genuine group-level properties (Chudek and Henrich 2014) or even group-level cultural transmission (Laland et al. 2000, 138).

https://doi.org/10.1086/688934 Published online by Cambridge University Press

2.5. Studies of the Origin of Culture. Finally, a small but significant amount of cultural evolutionary science is aimed at understanding the origin of culture (Boyd and Richerson 1996; Richerson and Boyd 2000). This work, in particular, is focused on understanding why capacities for social learning, especially cumulative social learning in humans, might have evolved. There are two ways this work could be understood as describing the origin of human "culture." One way would be the origin of the mass of socially learned cultural traits and types of cultural evolutionary processes that humans have; it could also mean the origin of the human capacity for culture. However, it does seem to mean both: when Boyd and Richerson (1996), for example, ask "why culture is common but cultural evolution is rare" they are referring at least in part to the learned traits and the process. When they and other cultural evolutionists describe "culture" as an adaptation or as a trait that has evolved by natural selection (e.g., Richerson and Boyd 2005, 99–147; Mesoudi 2011, 190–91), they must mean the capacity for culture: while single cultural traits can be adaptations in the sense that some cultural evolutionary processes are adaptive, "culture" the adaptation is not any one individual-level cultural trait or even the mass of them, since neither of these things was the target of the natural selection process on which these scientists are focusing in this case. Instead, the target of this natural selection process was the mechanisms for social learning and related capacities that permit the acquisition of these cultural traits: for example, when Richerson and Boyd (2005) discuss why culture may or may not be an adaptation, their focus is on the capacity for social learning. The cumulatively socially learned and culturally evolved mass of information and the processes that produced it explain why the capacities evolved by natural selection, but they are not what evolved in this sense.

2.6. Why All These Different Uses of the Culture Concept? So far I have given some reason to think that there are multiple uses of the term "culture" in the cultural evolutionary sciences. The question is what in fact explains the different ways these terms are being used. My contention is that the best way to understand this case is that there are in fact multiple culture concepts in the cultural evolution literature. There are, however, some alternative possibilities. One is that the different uses indicate the presence of different scientific projects and that as a matter of fact what I have been treating as a relatively unitary field (cultural evolution) is much more disparate than supposed. For example, culture might be used to refer to both culture in animals and culture in humans because there are two fields (animal culture and human culture fields) that use different culture concepts. This, however, does not seem to be the case. The different uses above occur within the work of particular researchers and overlap between them: for example, Laland, an important researcher in niche construction is an equally important researcher

https://doi.org/10.1086/688934 Published online by Cambridge University Press

of animal culture and has discussed at length human gene culture coevolution and group-level culture, sometimes within the same papers (Laland et al. 2000; Laland and Hoppitt 2003). Furthermore, the most plausible divisions in the cultural evolutionary sciences do not map onto the different uses above. For example, dual inheritance theorists and the epidemiology of representation researchers might plausibly differ on whether to understand individual-level culture in terms of representations, rather than behaviors, but in practice both groups use both versions of individual-level culture as described earlier. Their differences also would not explain the distinct appeals to group culture, individual culture, and niche-constructed environments described above, for example, since EoR researchers rarely deal with group or niche construction models. Instead, the different uses of the culture concept occur in different types of models and explanations, which deal with different, if related, phenomena.

However, the possibility that I want to consider in detail is that the different uses of "culture" and the phenomena they describe can in fact be gathered under some sufficiently broad single definition of culture. There are a variety of proposed culture concepts in the philosophical and cultural evolution literature that might be able to do the work. In the next section, I argue that, while we cannot completely rule out any such definition, at the very least, none of the current attempted definitions of culture can be successfully applied to all the uses of "culture" described above. This leaves the remaining possibility: that there are in fact distinct, if related, culture concepts.

3. Current Definitions of Culture. In the cultural evolution and the philosophy literature there are a number of proposed culture concepts: these include informational concepts of culture and phenotypic concepts of culture, which in turn include culture as mental representations or ideas and culture as behavior.

3.1. Culture as Information. I want to begin with what I think is the most intuitively obvious way to define culture, in terms of *information*. One property shared by all of the various entities or phenomena that anyone wants to count as "culture" is that they carry, transmit, or help to transmit information. The definition of culture in terms of information is extremely popular in the cultural evolution literature. For example, Richerson and Boyd describe culture as "information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social learning" (2005, 5) that can also be present in artifacts or the environment; Mesoudi et al. (2006, 331) largely follow Richerson and Boyd's definition. However, the notion of information used in these definitions is essentially disposable: these authors often say that by

https://doi.org/10.1086/688934 Published online by Cambridge University Press

"information capable of affecting behavior" they mean, essentially, mental states of various kinds (Richerson and Boyd 2005, 5; Mesoudi 2011, 4). Consequently, I will include these authors in the next section, "Culture as Phenotypic Traits." By far the best remaining candidate for a genuinely information-based account of culture is Ramsey (2013). Ramsey defines culture (partly following Mesoudi 2011) as "information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, [a] behavioral trait" (Ramsey 2013, 466). So while culture is clearly necessarily either a kind of information or an information-bearing state, activity, or property, not just any such information or state is culture; Ramsey claims the appropriate limitation is that cultural information *travels through a behavioral channel* (466).

Ramsey's purpose in giving a definition of culture is not necessarily to unify the various cultural phenomena described in the cultural evolutionary literature, but he does seem to be aware of the different phenomena involved: for example, he takes seriously the idea that there is cultural information present in niche-constructed environments and artifacts (2013, 466), and his appeal to groups in the definition suggests he takes seriously the idea that one could have group-level cultural traits. So could his definition actually do this work? Unfortunately, used for this purpose, his definition has a variety of problems. The first problem is that the definition is not going to successfully handle group-level culture. While individual-level culture plausibly "flows through a behavioral trait" in that the performance of an individual-level cultural behavior is required for social learning to occur and for that behavior to be reproduced, the same is not true of group-level behavior. While there is some reasonable sense to be made of the notion of a group-level behavior (e.g., a group ritual), that behavior is reproduced by the individual-level social learning of its component individual-level behaviors and not necessarily by observation (or anything else) of the group-level behavior as such. Hence, the group-level "behavior" that is reproduced is not necessarily the behavior through which cultural information flows.

The second problem for Ramsey is that he defines culture in terms of information itself, rather than in terms of information carriers, such as behaviors, mental representations, artifacts, or environments. This does raise an important issue: as Sperber and Claidiere (2008) note, information as such has no causal power; instead, it is the carriers and processors of information that generate behavior and have the other effects attributed to culture. This means cultural information as such cannot cause behavior, changes in the environment, and so on, as most cultural evolutionary explanations suggest it can. Ramsey's main reason for this move is that he wants to maintain a distinction between cultural and genetic causes of traits in which cultural traits are those for which cultural information (vs. genetic information) is

https://doi.org/10.1086/688934 Published online by Cambridge University Press

the primary difference maker in their origin; if culture is to be the cause of phenotypic traits, it cannot also be those traits themselves. The problem with making this distinction, as Lewens (2015) argues, is that Ramsey offers us no clear way to make sense of the notion of genetic versus cultural information, except via the notion of a cultural *channel*, but there is similarly no clear way to demarcate a cultural channel from a genetic one. Lewens also suggests that cultural traits can be caused by culture in the sense that they are caused by the cultural traits of other people (via social learning), so the phenotypic definition of culture can be preserved even in the face of this requirement.

The third problem with Ramsey's definition for capturing the evolutionary culture concept is that it is just too broad. While Ramsey takes seriously the need to account for multiple types of cultural transmission and information, he includes as culture any information that "flows through a behavioral channel" so long as it reproduces the behavior in the appropriate way. Ramsey's reason for this looseness is that he deliberately wants to include epigenetically transmitted behaviors in "culture" where the epigenetic change leading to the behavior in the offspring is caused by the same behavior in the parent. This means that even if his definition could account for most cultural phenomena described in section 2, it would not be a definition of culture as used by the cultural evolutionary scientists. The reason is that these scientists are focused on understanding a cluster of phenomena that involve the spread of informational states via social learning as such, rather than merely via behavior. Ramsey chooses to avoid definitions of culture in terms of social learning because the concept of social learning is not very well defined (as discussed earlier, social learning and individual learning form a rather fuzzy continuum), but in so doing he makes his definition something rather different from what is currently being used in the main scientific programs studying cultural evolution. While this may be his intent—this may be as much a prescriptive as a descriptive proposal—it does mean that this definition will not do the work needed to account for the uses of culture in the cultural evolutionary literature.

3.2. Culture as Phenotypic Traits. Views of culture as phenotypic states are fairly common in the cultural evolution literature. There are some differences, however, in which phenotypic states are taken to be culture. The most common view is that culture is socially transmitted mental representations. The individuals most explicitly holding this view are those evolutionary psychologists and cognitive anthropologists who advocate an EoR view of culture (e.g., Tooby and Cosmides 1992; Boyer 1999; Atran 2001; Sperber and Claidiere 2008); memeticists such as Dawkins (1999); some of the dual inheritance theorists such as Durham (1991, 3–5), who defines culture as "shared ideational phenomena"; and some evolutionary behavioral economists, such as Bowles and Gintis (2011, 13) who define culture in

https://doi.org/10.1086/688934 Published online by Cambridge University Press

terms of preferences and beliefs. We can add to these many of the "culture as information" theorists such as Richerson and Boyd (2005) and Mesoudi et al. (2006) who, as shown previously, take cultural information "in brains" to really refer to socially learned mental representations or similar states.

However, it is also possible to take culture to be socially learned behavior. Behavior here can be read as overt behavior—actual movements—patterns of behavior, or behavioral dispositions. A few individuals hold an at least partly behavioral view in the literature: for example, Jablonka and Lamb, define behavioral culture as "a system of socially transmitted patterns of behavior, preferences and products of animal activities that characterize a group of social animals" (2005, 160). Finally, one can take culture to be (at least sometimes) socially learned or transmitted artifacts, as proposed in part by Dawkins (1999), Richerson and Boyd (2005, 63), and Sterelny (2012).

The question, then, as with the previous definition of culture, is whether these kinds of definitions can capture the range of uses of the culture concept described in section 2. Let us first consider how well they do at making sense of the way the concept of culture is used in individual-level work. As I discussed earlier, in practice, real individual-level cultural evolutionary models use a variety of these different phenotypes as their focus in different cases. So in determining how well such phenotype-based definitions of culture account for scientific practice, we need to explain why these differences arise. One possibility is that one type of phenotypic definition is right, and the others are either wrong or operationalizations of that one; another possibility is that it genuinely varies from case to case which sort of phenotype is the "right" focus of the model; another possibility is that they are simply equivalent, and the variations are just a matter of preference. In favor of this last view, many cultural lineages involve social learning in which behaviors or artifacts are "copied" to form mental states, which produce behaviors, which produce artifacts, which are "copied" to form a new generation of mental states, and so on; each component is necessarily part of the cultural lineage, and each gets "reproduced" to some extent.

So why think that one type of cultural trait in these sequences is what is really reproduced and the others are not? One argument that has arisen in the memetics literature is that the mental representations view of culture permits a natural parallel between cultural and genetic evolution: there is a "replicator" and an "interactor" in both cases. In the genetic case it is the genes and the phenotype, and in the cultural case the mental representation and the resultant behaviors or artifacts (Hull 1988). The claim is that mental representations are then what "really" evolves and is reproduced across generations (Dawkins 1999). However, it is not clear why this distinction is important; even in some biological evolutionary processes (e.g., codon bias or meiotic drive), the so-called replicators are also the interactors.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

Another way that arguments have been run for preferring the mental representations view over the behavior or artifact view is that most human social learning processes reproduce one or the other "properly" at the expense of the other. The argument is usually that the behaviors and artifacts produced in cultural lineages tend to be error prone relative to what is intended by their producers. Individuals reproducing these behaviors or artifacts often correct for these errors: they reconstruct what is intended (the mental representation of the producer), rather than what is actually produced (Sperber 2000). However, this will not decide the issue either. While behaviors may be error prone, mental representations are invisible: the only way to "copy" mental representations is via observing the behavior they produce, and hence these mental representations may also be error filled. Furthermore, the idea that copying accuracy determines what is really forming cultural lineages is mistaken: cultural transmission can occur even in the face of imperfect replication (Henrich, Boyd, and Richerson 2008).

However, if we do take the view that one "culture as phenotype" view is correct and the others are not, then we have to account for why we see different uses of behavior, artifacts, and mental representations in different models (see the examples given in sec. 2.1). One possible reason is that the different views of culture are simply *operationalizations* of a more specific culture concept: cultural information cannot be observed directly, whereas the particular phenotypic traits that carry it can. As one might expect if this were true, the notion of "culture" used depends to some extent on the type of explanation being used: for example, cultural evolutionary scientists are more likely to use models describing artifacts as opposed to behavior when the behaviors are inaccessible in themselves apart from the artifacts (Henrich 2004). However, some of these cultural evolutionary models and explanations are abstract "proofs of concept": as such, the appropriate forms of testing for these models do not involve observations of either behaviors or mental states but instead things like mathematical simulations of populations, and so on; consequently, there is no need to operationalize (e.g., Claidiere and Sperber 2007; Henrich and Boyd 2008). Nevertheless, it is behaviors, rather than mental representations, that are still what is described on the models.

Most of the previous cases have been based on dividing up the same lineages into their behavior, mental representation, or artifact parts and then deciding that one or the other of these is the "real" culture in all cases. However, Jablonka and Lamb's (2005) discussion of "symbolic culture" suggests another problem for this way of thinking. Consider, for example, a lineage of cakes baked by individuals on the basis of the same recipe. In practice, many disparate types of things may form parts of such a cake lineage: actual cakes, recipe-describing linguistic behavior, artifacts (recipe cards or books), mental

https://doi.org/10.1086/688934 Published online by Cambridge University Press

states (mental representations of recipes), and cake-baking behaviors. While there is always a mind-behavior-mind or mind-behavior-artifact-mind pattern in these lineages, the behaviors and artifacts in each such sequence may be different. For example, the sequence might go from the mental representation of a recipe (in one person) to cake-baking behavior to cake to the mental representation of recipe (in the next person) to speaking of recipe to mental representation of recipe (in the third person) to writing behavior to recipe card to mental representation (in the fourth person), and so on. So why (and how) are such different components making up these lineages? It is worth noting that, when the behaviors and artifacts in these lineages are not actually the cake or cake-making behaviors themselves, they are symbolic/linguistic items meant to induce the same *mental content* as observing the cake-making behavior would, that is, to reproduce the mental representation of the recipe in the absence of the cake. One natural interpretation of these cases is that in some chunks of the lineage what is being reproduced is a cake (an artifact) or the cake-making behavior; in others it is the mental representation of the recipe. Jablonka and Lamb describe the former as "behavioral culture" and the latter as "symbolic culture." Any definition of culture in terms of only one particular sort of phenotype may automatically exclude these natural ways of thinking about such cases. A well-formulated culture concept should perhaps not be so specific.

Of course, the discussion so far in this section simply relates to how well phenotypic definitions of culture capture the individual-level culture concepts used in cultural evolutionary models. How about culture as behavior and culture as mental representations and their capacity to deal with cases of group-level culture? Culture as mental representations is going to have trouble here. Group-level traits, of the sort described earlier, are certainly caused by or composed of individuals' mental representations and behaviors, but they are not simply those representations; there is also not a group-level mind. It is plausible, alternatively, that there are genuinely group-level behaviors or artifacts; however, group-level traits are not "socially learned" or, at least, not in the same way as individual-level traits are and the above definitions suggest. In fact, Jablonka and Lamb (2005) get around this problem by defining behavioral culture entirely in terms of patterns of behavior characterizing groups and avoid the individual- versus group-level distinction altogether.

Similarly, the culture as mental representations concept falls short in dealing with cases in which culture is a transmitted environment. If culture is mental representations, then it cannot possibly exist in nonmental environments; transmitted environments are caused by behaviors, rather than being those behaviors. "Culture as artifacts" could possibly work here as long as artifacts are read to include transmitted environments, but of course it will have problems capturing the other uses of "culture." It is probably best, therefore, to take these "culture as phenotype" views to be, at best, attempts to formalize

https://doi.org/10.1086/688934 Published online by Cambridge University Press

a definition of individual-level culture and not applicable to any of the other uses of the culture concept.

4. The Evolutionary Culture Concepts. What I hope the previous discussion has established is that the current proposals for definitions of culture are not going to be able to unite the various forms of culture currently described in the evolutionary social sciences. Given the previous discussion, this leaves us with one remaining possibility: there is no single definition of the evolutionary culture concept, and instead "culture" in the cultural evolution literature can refer to the various members of a family of related concepts that share a variety of overlapping features or other relevant connections. In this section I want to describe what I think are the most important members of this family.

The most obvious of these culture concepts is the individual-level culture concept. The most important scientific function of this concept is its role in descriptions and explanations of the cultural evolutionary phenomena that happen within human populations and its role in capturing the relationships between human and nonhuman animal culture. One important purpose of explicating these relationships is to explain the evolutionary function of human culture and (therefore, in part) its origins and history. This in turn connects individual-level culture with culture understood as the psychological adaptations that permit social learning and transmission.

Individual-level culture then is best understood as *socially learned, potentially lineage forming, information-carrying phenotypic traits*. Social learning is clearly the feature of culture most important for explaining its origins; it permits the reduced learning costs and (especially cumulative) population-level processes that make culture worthwhile for those animals that possess it (especially humans). Every type of culture described by the cultural evolutionists either is, processes, is made by, or is composed of informational states, but as I argued earlier, culture must consist of the traits that carry information rather than the information itself if it is to have any causal effects; since these must also be transmitted via social learning, these will generally be either psychological traits, behaviors, or artifacts. However, given the different ways that individual-level culture behaves, it makes sense to not limit this definition of culture to any one of these sorts of phenotypes and to leave it as a matter of scientific investigation how these sorts of states operate in cultural transmission. Finally, generally speaking, cultural evolutionary traits must at least potentially be able to form lineages.[4] Social learn-

4. This notion of individual culture may seem too restrictive: occasionally cultural evolutionary scientists speak as though all mental representations acquired from social learning count as culture, not just the ones that manage to form lineages. I suggest a separate term for these traits that "stay in the learner's head": *idioculture*.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

ing, especially in humans, often involves individuals choosing between cultural traits, and hence some never actually form lineages; furthermore, as described earlier, in a few cases cultural processes may not involve clear lineages at all (Henrich et al. 2008). Nevertheless, most cultural evolutionary processes do involve competing lineages in the causal sense described earlier.

As I have argued, however, the phenomena studied in cultural evolutionary science go beyond just individual-level culture: there are at least three further types of culture, which are group culture, environmental culture, and cultural psychology. Group culture can be defined as traits of groups that are composed of the individual-level culture of the members of those groups, such that those traits have or had some evolutionary or functional effects in their own right, which potentially affect the fate of the group and that are not simply reducible to the individual-level cultural traits that compose them. The reason for this second requirement is that we would not want to call "culture" all group-level properties that are composed of individual-level culture. Instead, group-level phenomena become of interest to cultural evolutionary scientists once they have functional or other evolutionary effects in their own right, and those effects potentially or actually could involve those groups in genuinely group-level evolutionary processes.

To understand how this definition applies, consider the main subtypes of group-level culture described in section 2: simple group-level cultural traits are composed of aggregations of individual-level cultural traits but nevertheless can potentially be subject to group-level evolutionary forces that conflict with those at the individual level (Sober and Wilson 1998). There are also more complex group-level traits or organizations composed of different interacting individual-level parts: these too can have their own functional properties, which potentially could benefit (or hinder) the group in competition with other groups (Wilson 2002). This does not require that the outcome of these group-level processes be felt at the level of the group. Both MLS1 and MLS2 forms of group selection involve real group-level forces (Okasha 2006); it is simply more obvious that group-level culture is a distinct phenomenon in MLS2 cases, where both forces and outcomes are felt at the group level. Finally, in the case of cultural phylogenetic explanations, what is being studied is the relationship between group-level traits in the form of the cultural traditions evident in groups. These traditions are more than merely individual-level traits or even individual-level lineages and undergo their own evolutionary processes of splitting and merging, which cultural phylogenetic studies seek to understand (see, e.g., Jordan and Shennan 2003). Having a concept of group-level culture, therefore, allows cultural evolutionary scientists to describe and take seriously the effects of group-level cultural evolution, to explain individual-level phenomena in terms of group-level effects or organization, and to explain the historical relationships between groups.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

Environmental culture, like group culture, is extremely various and includes both artifacts and environmental changes produced by individual-level or group culture. Environmental culture is that set of artifacts and environmental changes that are the consequences of the socially learned behavior of individuals either alone or in groups, but where those behaviors are learned or transmitted because they produce those environmental changes and where the artifact or environmental change either is reproduced or persists such that it potentially can have an effect on the evolution of its producers or others. The first requirement is what makes it environmental *culture* as opposed to other forms of environmental change or niche construction. The second requirement makes it clear that environmental culture is not one of the myriad incidental consequences of the individual-level cultural behavior. The "because" can, however, be read relatively broadly: it can refer to deliberate learning or teaching to produce an outcome, or it can be causal in that the environmental changes themselves might promote the acquisition of behavior that leads to their reproduction (in the next iteration). Mere deliberateness, however, is not enough to make something culture. To be culture, it must not be the one-off and ephemeral creation of an individual (or even a group), but instead it must continue to interact with the group or lineage that produces it, either by persisting or by being reproduced; as with group culture, the "interaction" effect for the cultural evolutionists is a functional or fitness effect that changes the outcome of the cultural or biological evolution of the individual or groups that is or were responsible for it (as above, because some group-level selection involves growth or persistence of the group rather than reproduction, that evolutionary effect may also be felt at the level of the individual or the group).

Finally, there is cultural psychology. Cultural psychology consists of the psychological mechanisms, representations, and other systems that direct social learning and permit cultural processes. These systems may be unique biological adaptations for the purpose of social learning (see, e.g., Henrich and Gil-White 2001), they may include mechanisms exapted for social learning that did not originally evolve for that purpose, or they may indeed be relatively simple changes in perceptual psychology or motivation that permits individual learning to become social learning (Heyes 2012). They may also involve structured, socially transmitted environments that permit social learning mechanisms to operate effectively (Sterelny 2012). Cultural learning psychology is, ultimately, the concept of culture that ties all the rest together. The presence of cultural learning psychology is necessary for the acquisition of individual-level culture; it is thereby ultimately responsible for group culture and produces environmental culture where the behavior it ultimately acquires interacts with and changes the environment in transmissible ways. At the same time, the activity of cultural learning psychology may have been modified by and certainly influenced by the nature of group and environmen-

https://doi.org/10.1086/688934 Published online by Cambridge University Press

tal culture. Even minimal cultural learning psychology might result in powerful social learning when in contact with the sorts of constructed and scaffolded learning environments that can make up environmental culture.

5. Conclusion. This article has argued that there are multiple concepts of culture used in the cultural evolution literature and that none of the explicit definitions of culture considered can account for how these concepts are used. I have endeavored to describe some of the main forms these phenomena take in the previous section. The final question we need to ask is why there is this variety of culture concepts and whether this is a productive situation for these sciences. In answering this question, it seems natural to consider the situation in other scientific programs in which there is a similar elasticity in common concepts—some of the most obvious being the "gene" and "species" debates (Griffiths and Stotz 2007; Ereshefsky 2014). For example, the consensus among philosophers of science is that there is a range of different concepts of "gene" being used in biology. These different concepts exist because, as the relevant fields have developed, the reference of the term has been adjusted and expanded slowly, in part as it is used in different kinds of work, for example, in the "gene" case the move from breeding and population experiments to molecular studies of different kinds, among other things (Burian 1985). "Gene" now refers to a variety of closely related but distinct phenomena in different areas of biology, such as those at different levels of description (population vs. molecular concepts) or perhaps different components of the genetic system (such as the coding sequence or the edited mRNA), and new concepts have been added as scientists have learned more about what is involved in the evolutionary, inheritance, and developmental mechanisms in which they are interested. Consequently, some philosophers have argued that the various gene concepts may really fall under a more general gene concept that is a prototype rather than a single rigid definition (Stotz and Griffiths 2004), and others in fact take the very elasticity in the concept to be beneficial to the progress of the field (Burian 1985). In much the same way, "culture" seems to be rather elastic and is applied to new phenomena as scientists consider culture at different levels of description (group vs. individual) or parts of the system (environmental vs. individual) and what, in different contexts, is undergoing the evolutionary and population processes that originally drew their attention. It is also possible that in much the same way there is a general concept of culture that unites the definitions above but that is also like a prototype, rather than definition (although establishing this is somewhat beyond the scope of this article). As such, it seems the absence of a single definition of culture is not a matter of any concern and may be beneficial; it is a feature of other important scientific concepts and exists because of the increasing understanding of cultural evolutionary processes in the cultural evolutionary sciences.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

REFERENCES

Aoki, Kenichi, and Marcus W. Feldman. 2013. "Evolution of Learning Strategies in Temporally and Spatially Variable Environments: A Review of Theory." *Theoretical Population Biology* 91:3–19.

Aoki, Kenichi, Mitsuo Shida, and Nanako Shigesada. 1996. "Travelling Wave Solutions for the Spread of Farmers into a Region Occupied by Hunter-Gatherers." *Theoretical Population Biology* 50:1–17.

Atran, Scott. 2001. "The Trouble with Memes: Inference Verses Imitation in Cultural Creation." *Human Nature* 12 (4): 351–81.

Blackmore, Susan. 1999. *The Meme Machine*. Oxford: Oxford University Press.

Bowles, Samuel. 2006. "Group Competition, Reproductive Leveling, and the Evolution of Human Altruism." *Science* 314:1569–72.

Bowles, Samuel, and Herbert Gintis. 2011. *A Cooperative Species: Human Reciprocity and Its Evolution*. Princeton, NJ: Princeton University Press.

Boyd, Robert, and Peter J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

———. 1996. "Why Culture Is Common, but Cultural Evolution Is Rare." *Proceedings of the British Academy* 88:77–93.

Boyer, Pascal. 1999. "Cognitive Tracks of Cultural Inheritance: How Evolved Intuitive Ontology Governs Cultural Transmission." *American Anthropologist* 100 (4): 876–89.

Burian, Richard M. 1985. "On Conceptual Change in Biology: The Case of the Gene." In *Evolution at a Crossroads*, ed. D. Depew and B. Weber, 21–42. Cambridge, MA: MIT Press.

Chudek, Maciej, and Joseph Henrich. 2014. "Tackling Group-Level Traits by Starting at the Start." *Behavioral and Brain Sciences* 37 (3): 257–58.

Claidiere, Nicolas, and Dan Sperber. 2007. "The Role of Attraction in Cultural Evolution." *Journal of Cognition and Culture* 7:89–111.

Dawkins, Richard. 1999. "Foreword." In *The Meme Machine*, ed. S. Blackmore, vii–xvii. Oxford: Oxford University Press.

Durham, William H. 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford, CA: Stanford University Press.

Eren, Metin I., Briggs Buchanan, and Michael J. O'Brien. 2015. "Social Learning and Technological Evolution during the Clovis Colonization of the New World." *Journal of Human Evolution* 80:159–70.

Ereshefsky, Mark. 2014. "Consilience, Historicity, and the Species Problem." In *Evolutionary Biology: Conceptual, Ethical, and Religious Issues*, ed. R. P. Thompson and D. Walsh, 65–86. Cambridge: Cambridge University Press.

Feldman, Marcus W., and Kevin N. Laland. 1996. "Gene-Culture Coevolutionary Theory." *Trends in Ecology and Evolution* 11 (11): 453–57.

Fracchia, Joseph, and Richard C. Lewontin. 1999. "Does Culture Evolve?" *History and Theory* 38 (4): 52–78.

Galef, Bennett G., Jr. 1992. "The Question of Animal Culture." *Human Nature* 3 (2): 157–78.

Griffiths, Paul, and Karola Stotz. 2007. "Gene." In *The Cambridge Companion to the Philosophy of Biology*, ed. D. L. Hull and M. Ruse, 85–102. New York: Cambridge University Press.

Henrich, Joseph. 2004. "Demography and Cultural Evolution: How Adaptive Cultural Processes Can Produce Maladaptive Losses—the Tasmanian Case." *American Antiquity* 69 (2): 197–214.

Henrich, Joseph, and Robert Boyd. 1998. "The Evolution of Conformist Transmission and the Emergence of between-Group Differences." *Evolution and Human Behavior* 19:215–41.

———. 2001a. "Weak Conformist Transmission Can Stabilize Costly Enforcement Norms in Cooperative Dilemmas." *Journal of Theoretical Biology* 208:79–89.

———. 2001b. "Why People Punish Defectors: Weak Conformist Transmission Can Stabilize Costly Enforcement of Norms in Cooperative Dilemmas." *Journal of Theoretical Biology* 208 (1): 79–89.

———. 2002. "On Modeling Cognition and Culture." *Journal of Cognition and Culture* 2:87–112.

———. 2008. "Division of Labor, Economic Specialization, and the Evolution of Social Stratification." *Current Anthropology* 49 (4): 715–24.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

Henrich, Joseph, Robert Boyd, and Peter J. Richerson. 2008. "Five Misunderstandings about Cultural Evolution." *Human Nature* 19:119–37.
Henrich, Joseph, and Francisco J. Gil-White. 2001. "The Evolution of Prestige: Freely Conferred Deference as a Mechanism for Enhancing the Benefits of Cultural Transmission." *Evolution and Human Behavior* 22:165–96.
Heyes, Cecilia. 2012. "What's Social about Social Learning?" *Journal of Comparative Psychology* 126 (2): 193–202.
Hull, David. 1988. "Interactors vs. Vehicles." In *The Role of Behavior in Evolution*, ed. H. C. Plotkin, 19–50. Cambridge, MA: MIT Press.
Ingold, Tim. 2007. "The Trouble with 'Evolutionary Biology.'" *Anthropology Today* 23 (2): 13–17.
Jablonka, Eva, and Marion J. Lamb. 2005. *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral and Symbolic Variation in the History of Life*. Cambridge, MA: MIT Press.
Jordan, Peter, and Stephen Shennan. 2003. "Cultural Transmission, Language, and Basketry Traditions amongst the California Indians." *Journal of Anthropological Archaeology* 22 (1): 42–74.
Laland, Kevin N., and Gillian R. Brown. 2002. *Sense and Nonsense*. Oxford: Oxford University Press.
Laland, Kevin N., and William Hoppitt. 2003. "Do Animals Have Culture?" *Evolutionary Anthropology* 12 (3): 150–58.
Laland, Kevin N., John Odling-Smee, and Marcus W. Feldman. 2000. "Niche Construction, Biological Evolution and Cultural Change." *Behavioral and Brain Sciences* 23:131–75.
———. 2001. "Cultural Niche Construction and Human Evolution." *Journal of Evolutionary Biology* 14:22–33.
Lewens, Tim. 2015. *Cultural Evolution: Conceptual Challenges*. Oxford: Oxford University Press.
Lycett, Stephen J., Mark Collard, and William C. McGrew. 2009. "Cladistic Analyses of Behavioural Variation in Wild Pan Troglodytes: Exploring the Chimpanzee Culture Hypothesis." *Journal of Human Evolution* 57:337–49.
Lycett, Stephen J., and Noreen von Cramon-Taubadel. 2008. "Acheulean Variability and Hominin Dispersals: A Model-Bound Approach." *Journal of Archaeological Science* 35 (3): 553–62.
Matthews, Luke, Jamie Tehrani, F. Jordan, and Mark Collard. 2011. "Testing for Divergent Transmission Histories among Cultural Characters: A Study Using Bayesian Phylogenetic Methods and Iranian Tribal Textile Data." *PLoS ONE* 6 (4): 1–10.
Mesoudi, Alex. 2011. *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*. Chicago: University of Chicago Press.
Mesoudi, Alex, Andrew Whiten, and Kevin N. Laland. 2006. "Towards a Unified Science of Cultural Evolution." *Behavioral and Brain Sciences* 29:329–47.
Odling-Smee, John, and Kevin N. Laland. 2011. "Ecological Inheritance and Cultural Inheritance: What Are They and How Do They Differ?" *Biological Theory* 6:220–30.
Odling-Smee, John, Kevin N. Laland, and Marcus W. Feldman. 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.
Okasha, Samir. 2006. *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
Ramsey, Grant. 2013. "Culture in Humans and Other Animals." *Biology and Philosophy* 28:457–79.
Richerson, Peter J., and Robert Boyd. 2000. "Climate, Culture and the Evolution of Cognition." In *The Evolution of Cognition*, ed. C. Heyes and L. Huber, 329–46. Cambridge MA: MIT Press.
———. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
Sober, Elliott, and David Sloan Wilson. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.
Soltis, Joseph, Robert Boyd, and Peter J. Richerson. 1995. "Can Group Functional Behaviors Evolve by Cultural Group Selection?" *Current Anthropology* 36 (3): 473–83.
Sperber, Dan. 1996. *Explaining Culture: A Naturalistic Approach*. Oxford: Blackwell.
———. 2000. "An Objection to the Memetic Approach to Culture." In *Darwinizing Culture: The Status of Memetics as a Science*, ed. R. Aunger, 163–73. Oxford: Oxford University Press.
Sperber, Dan, and Nicolas Claidiere. 2008. "Defining and Explaining Culture: Comments on Richerson and Boyd, *Not by Genes Alone*." *Biology and Philosophy* 23:283–92.
Sterelny, Kim. 2012. *The Evolved Apprentice*. Cambridge, MA: MIT Press.

https://doi.org/10.1086/688934 Published online by Cambridge University Press

Stotz, Karola, and Paul Griffiths. 2004. "Genes: Philosophical Analyses Put to the Test." *History and Philosophy of the Life Sciences* 26 (1): 5–28.

Tooby, John, and Leda Cosmides. 1992. "The Psychological Foundations of Culture." In *The Adapted Mind*, ed. J. H. Barkow, L. Cosmides, and J. Tooby, 19–136. Oxford: Oxford University Press.

Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, and C. Boesch. 2001. "Charting Cultural Variation in Chimpanzees." *Behaviour* 138:1481–1516.

Whiten, Andrew. 2000. "Primate Culture and Social Learning." *Cognitive Science* 24 (3): 477–508.

Wilson, David Sloan. 2002. *Darwin's Cathedral: Evolution, Religion and the Nature of Society*. Chicago: University of Chicago Press.

https://doi.org/10.1086/688934 Published online by Cambridge University Press