

What is animal culture?

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Culture from humans to nonhuman animals

Culture in humans connotes tradition, norms, ritual, technology, and social learning, but also cultural events like operas or gallery openings. Culture is in part about what we do, but also sometimes about what we ought to do. Human culture is inextricably intertwined with language and much of what we learn and transmit to others comes through written or spoken language. Given the complexities of human culture, it might seem that we are the only species that exhibits culture.

How, then, are we to make sense of culture in animals?¹ The study of animal culture is a booming research area. Culture is said to occur in a wide range of vertebrates from our close kin, chimpanzees (Whiten et al. 1999) and orangutans (van Schaik et al. 2003), to more distant relatives like rats (Galef and Aleen 1995) and whales (Whitehead and Rendell 2015). Could these studies be misleading in that they are not actually studying culture but simply misapplying the term ‘culture’? Or is what is labeled culture in animals at the core of human culture, so that although human culture is more elaborate than animal culture, it is different in degree, not kind? While it is certainly easy to intentionally define culture in a way that makes it unique to humans, because of the growing field of animal culture, it would be most useful to attempt to offer a definition of culture that makes sense of how it is used by psychologists, biologists, anthropologists, and others who use the term culture in studies of animal behavior. The challenge is to produce a concept that is broad enough to be able to apply across humans and animals, but not be so anemic that it cannot do justice to human culture. Because of this, I will here construct a definition of animal culture and draw out some of its implications. Let’s begin by considering what ingredients should go into such a definition.

¹ Nonhuman animals, that is—I will for simplicity use ‘animals’ to denote nonhuman animals.

Ingredients for a definition of culture

Anthropology has a long tradition of proposing definitions of culture. Kroeber and Kluckhohn (1952) tallied 164 definitions, and many more have been added in the subsequent half century. Some of the definitions of culture focus on cultural products, like Tyler's (1871) understanding of culture as a “complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society” (1). Others focus on social learning or heredity: “*culture* means the social heredity of mankind” (Linton 1936: 78). Still others define culture not in terms of outcomes, but instead in terms of the information that governs behavior and helps create cultural products: “culture is best seen not as complexes of concrete behavior patterns—customs, usages, traditions, habit clusters—as has, by and large, been the case up to now, but a set of control mechanisms—plans, recipes, rules, instructions (what computer engineers call “programs”)—for the governing of behavior” (Geertz 1973: 44).

Given this diversity of definitions, should we sift through them and try to determine which one is correct? I am inclined not to attempt to pick out the correct one(s), casting others aside. Instead, most of the definitions get at important features of culture. Culture is a form of social heredity, it is something that governs behavior, and it is something that forms the basis of traditions and artifacts. The challenge is not to find the right (or best) definition from those available, but to pick out the essential ingredients of culture and then figure out how to put them together to produce a synthetic definition of culture. Kroeber and Kluckhohn attempted to do just that when they proposed that culture “consists of patterns, explicit and implicit, of and for behavior acquired and transmitted by symbols, constituting the distinctive achievement of human groups, including their embodiments in artifacts; the essential core of culture consists of traditional (i.e., historically derived and selected) ideas and especially their attached values; culture systems may, on the one hand, be considered as products of action, on the other hand, as conditioning elements of further action” (1952: 357). Their definition has the merit of trying to put together important ingredients, but it is of little help for animal culture since it defines culture in terms of humans. And while human culture is clearly highly symbolic and value-laden, these features do not seem to be necessary conditions of culture. For producing the ingredients for a synthetic definition of animal culture, let's consider how animal culture is often understood.

In animal behavior studies, culture often has a negative, operational definition: If there is

a behavioral difference across populations that is not explainable in terms of environmental or genetic differences, then it can be attributed to culture. But culture is sometimes given explicit positive definitions as well, for example, “a cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic” (Whiten et al. 1999: 682). Note that this is not so much a definition of culture, but instead a characterization of a prototypical result of culture. As such, it features characteristics that are commonly associated with culture, like being population-wide, but not necessarily ones we should use as a base for a definition of culture. Similarly, although many genes are homogeneous across populations, it would be misleading to define what genes are in terms of population-level phenotypic characteristics.

Defining culture in terms of outcomes like traditions or group typicality is widespread in the animal culture literature. For example, Allen et al. (2013: 485) define culture in terms of “shared behavior propagated by social learning,” and Laland and Janik (2006: 524) understand “culture (or tradition) as all group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information.” To understand the various components of the way animal culture is commonly defined in the literature, let’s unpack Laland and Janik’s definition.

Laland and Janik’s definition utilizes three main ingredients. One is an *outcome*, a “group-typical behaviour pattern.” Not all behavioral group typicality is cultural, of course, but as they have defined culture, group typicality is a necessary but not sufficient condition for culture. The second ingredient is a *mechanism*; the behaviors are in part due to the mechanism of social learning. The third ingredient is the thing passed on, the *content*, which they describe as “transmitted information.” It is rather cumbersome to define culture in terms of outcome, mechanism, and content. Is this complexity necessary or can we perhaps jettison some of the ingredients? As mentioned above, group typicality is not a desired criterion for culture since it eliminates any cultural variants that are not group-typical, and there is nothing necessary about culture that makes it have to be typical of—or common in—the group. It might, then, be tempting to eliminate this criterion and have culture be defined not in terms of particular kinds of outcomes, but instead in terms of mechanism and content only. Thus, one might think that culture should be defined simply as socially transmitted information.

But to expunge group typicality would be to miss the point that it is inserted into the

definition to solve a problem. The problem is that not all information that organisms transmit from one another constitutes culture. Some is mere ephemeral communication—it has an effect on the recipient but not a lasting one or not one capable of supporting traditions. An alarm call may allow a macaw to learn of an approaching eagle from a conspecific, but what is socially learned by the macaw about the eagle's proximity is not something that forms the basis of a tradition. Similarly, one howling wolf might set the pack howling, but this is not the kind of behavior that is considered cultural. There thus must be a restriction in place, but one that does not require group typicality. I will turn to the question of a replacement restriction in the following section, but let's first consider the other two components, mechanism and content.

Social learning is a component of Laland and Janik's definition and is a common feature of culture definitions. Unfortunately, there are some difficulties with the social learning criterion. As Sterelny (2009) argues, "it is far from clear that there is a distinctive and identifiable form of learning, social learning, that contrasts with (say) individual trial-and-error learning in response to ecological circumstances" (295). And while social learning may be important for culture, it does not suffice for culture. McGrew (2009), for example, holds that "if culture equals social learning, then many creatures, e.g., octopus, guppy, and lizard, must be granted cultural status. If culture is more than social learning, then we must look elsewhere for essential criteria. On these grounds, it seems sensible to consider social learning as necessary but not sufficient for culture" (50). McGrew is certainly correct that social learning is not sufficient for culture. And social learning—or something like it—is necessary. The reason that social learning is a ubiquitous ingredient in definitions of culture is that cultural traditions are sustained by the information that is passed on from one individual to another through behavioral performances. Thus, we need not worry about what, precisely, counts as social learning, and can sidestep the issues raised by Sterelny. We can do so by simply recognizing that for information to be cultural, it must be transmitted from one individual to another via a behavioral channel.

The final ingredient is the content, what Laland and Janik label *information*. I agree with them that defining culture in terms of information is a good strategy. But one should be cautious. The term 'information' is used in a variety of ways—leaving it unspecified can lead to vacuity, while giving a detailed specification can lead to problems (Lewens 2014). But for the purpose of animal culture, what we want from a concept of information is the reduction of uncertainty. By this I don't mean the *feeling* of uncertainty and its associated anxiety. Instead, if there are

multiple ways for, say, a rat to extract seeds from pinecones, and that through the behavioral transfer of information, the number of ways that the rat might use is reduced (down to one, perhaps), then the uncertainty concerning seed extraction has been reduced. Similarly, in a shell game, you gain information about the hidden item by lifting one of the shells to the extent that the uncertainty in the item's whereabouts is reduced by seeing what is under a particular shell. This notion of information is what Dretske (1983) used and developed, and is related to the mathematical accounts of information arising from Shannon and Weaver (Shannon 1948; Shannon and Weaver 1949).

What animal culture is

Let's take stock of the ingredients. Laland and Janik are right that outcome, mechanism, and content are all important ingredients in a concept of animal culture, but there were difficulties with their specific interpretation of these. Let's begin with the last and work backward.

Information, suitably defined, seems to be an important part of a definition of culture. In fact, I would go further to argue that culture *is* information—it is a particular kind of information. The other two ingredients are not a part of what culture is, but instead are what help to delimit the kind of information that is culture. The second ingredient, mechanism, is an important way of delimiting this information, though since we are considering the flow of information, the term 'channel' may be more apt. Culture, then, is information transmitted from person to person (or between groups of people, since there may be some forms of cultural information that no individual possesses, but is possessed and transmitted by a group) along a particular kind of channel. The channel that the information must pass through is behavior—it must be transmitted by behavior and not, say, by genes. Thus, taking into account the last two ingredients, we can produce a preliminary, incomplete definition of culture as information transmitted between individuals or groups, where this information flows through the behavior.

From the above example of wolf howl contagion or the startling precipitated by an alarm call, it is clear that not all information that is passed through behavior between individuals or groups is culture. Instead, the outcome the information has is important for whether it is truly culture. In particular, the information must help to bring about the reproduction of the behavior that serves as a channel for the information, and it must have a lasting effect on the behavior of the recipient(s). This idea of culture causing, passing through, and reproducing behavior is not

too far from what Kroeber and Kluckhohn were getting at when they held that “culture systems may, on the one hand, be considered as products of action, on the other hand, as conditioning elements of further action” (1952: 357). We can now, following Ramsey (2013), put together the three ingredients into one definition: *Culture is information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, the behavioral trait.*

This definition has each of the three ingredients that are common in definitions of culture. But the definition offered here avoids the requirement that culture bring about behavioral homogeneity, and instead of using the somewhat vague and controversial concept of social learning, it simply specifies the channel through which the information must flow in order for it to count as culture. The definition also does not predetermine which taxa exhibit culture. If guppies, lizards, or octopuses transfer information amongst themselves in such a way that it flows through and brings about the reproduction of, and a lasting change in, a behavioral trait, then it is a cultural species. The question of whether or not this concept of culture applies to such taxa has an answer based on empirical evidence, not stipulation.

Culture, environment, and epigenetics

Cultural transmission, as defined here, is certainly distinct from genetic transmission, and cultural explanations of behavioral differences are distinct from and complementary to genetic explanations of difference. Environment, however, is not so easily or cleanly distinguished from culture. The reason is that there can be cultural artifacts and these artifacts can help furnish the environment. This implies that environment, genes, and culture do not represent three mutually exclusive sources of behavioral differences. Instead, environment is divided into cultural environment and acultural environment.

How, then, can part of the environment such as an artifact be cultural given the definition of culture provided above? The answer is that while culture necessarily flows through behavior, it can flow through other material things as well. A spear point is a result of behavior, but it can also serve as a channel for cultural information. One can learn some of how to build spear points through the examination of points fashioned by others. Thus, some of the uncertainty in how to build a particular kind of point is reduced through the inspection of such points. Objects become channels for information when they help recapitulate in others the behavior that shaped them.

Similarly, animal trails can be cultural artifacts—they decrease the uncertainty of their conspecific's walking behavior, and by walking on them they help to induce like behavior in others. The fact that environment and culture overlap does not mean that it is wrong to operationalize the detection of culture by eliminating environmental and genetic differences. Instead, what one needs to exclude in such assessments are features of the environment fashioned by individuals via cultural behavior. But in studies of culture in animals, this is typically done. For example, if orangutans on one side of a river eat a fruit that a group on the other side does not, what one looks for is whether the fruit is growing on both sides in a similar density and in areas that are similarly accessible.

Where things become more difficult is when there is a significant degree of niche construction (Odling-Smee et al. 2003). Niche construction occurs when organisms modify their environment in a way that can have ecological and evolutionary effects. Beavers building dams is a classic example—the result of their construction creates ponds, and swimming in the ponds they have constructed modifies their selection pressures. But such behavior is not cultural just because it involves niche construction. While there can be cultural niche construction, much niche construction occurs in the absence of culture. The litmus test for whether a part of the environment is cultural is whether its form and/or function is in part the result of a behavior, and whether its having this form and/or function leads others to reproduce in the environment a similar form or function.

Just as culture, as defined above, can flow *outside* of our bodies, it can also flow *inside* and can even affect how genes are transcribed. Being licked by one's mother affects a rat pup's epigenetics (Weaver et al. 2004). Rats that are licked as pups are therefore differently constituted and may therefore behave differently. If being licked as a female pup makes the rat tend to lick her own pups once she matures and eventually has offspring, then this licking behavior is cultural behavior. The licking behavior is traditional and could be disrupted by an intervention in which mother rats were prevented from licking their pups. Thus, even though the licking behavior is in part mediated by epigenetics, it is cultural nevertheless.

Culture and epigenetics are sometimes viewed as alternative ways to explain patterns of behavior. For example, Jablonka and Lamb (2005) distinguish epigenetic and behavioral inheritance mechanisms and place culture within behavioral inheritance only. But under the framework provided here, culture can flow through an epigenetic channel. It therefore follows

that culture and epigenetics—like culture and the environment—overlap and are not alternative, mutually exclusive ways of explaining behavioral patterns.

In a similar way, passing on dietary preferences in utero or through milk can count as culture (Galef and Sherry 1973). If the feeding behavior of the mother is reproduced in the young—that is, the dietary uncertainty of the offspring is reduced by the maternal diet—then cultural information flows through the mother’s behavior, into her gut, and via biochemical channels to her offspring. Such pathways, like cultural niche construction, can be long and tortuous but, according to the framework provided here, count as culture.

Criteria for recognizing culture in animals

Given the definition of culture offered here, it is natural to ask what observable criteria can serve as evidence of culture. In answering this question, let’s consider an influential way of testing for culture, that of McGrew (1992), to see how it compares to this definition. Instead of simply defining what culture is, McGrew offers a set of operational criteria that one can use to determine whether culture is present. He offers eight criteria, which he takes to be individually necessary and jointly sufficient for a species to be cultural: innovation, dissemination, standardization, durability, diffusion, tradition, non-subsistence, and naturalness. Let’s consider each in turn.

Innovation is described by McGrew as a “new pattern is invented or modified” (1992, p. 77). There is a growing literature on animal innovation (Reader and Laland 2003) and there is debate concerning how, precisely, we should understand the concept. It is clear that innovation can occur in the absence of culture and if, as McGrew argues, innovation is a necessary condition, then culture cannot exist without innovation. Using the framework provided by Ramsey, Bastian, and van Schaik (2007), while innovation may be the prime source of behavioral novelty, it may not be necessary for such novelty. Instead, mistakes can lead to behavioral novelty, or novel behaviors can be induced by the environment, and this novelty can be transmitted as a cultural tradition. Thus, it wrong to define culture in terms of innovation, but it may not be wrong to use innovation as an indicator of culture, since there is a good chance that they are empirically highly correlated.

Dissemination is described as “pattern acquired by another from innovator” (1992, p. 77). Because, as I just argued, there is no definitional link between innovation and culture, I think it is

wrong to define dissemination in terms of innovation. That said, because the flow of information in culture transmission is a form of dissemination, I agree with McGrew that dissemination—defined differently—is a necessary condition.

Standardization is described as “form of pattern is consistent and stylized” (1992, p. 77). To the degree that cultural information is conveyed from one individual to another behavioral standardization will ensue. Thus standardized behavior patterns will be a part of any cultural system. That said, consistent behavior patterns may be present with or without culture. Thus, such patterns by themselves bear scant evidence for culture.

Durability is described as “pattern performed outwith presence of demonstrator” (1992, p. 77). Durability here plays a similar role as that played by the “lasting change” in the behavioral trait, as described above. If the information has a lasting change on behavior, then it will be durable, it will be performed in the absence of the demonstrator.

Diffusion is described as “pattern spreads from one group to another” (1992, p. 77). While cultural species will often exhibit diffusion, I do not agree that one should take it to be a necessary condition for culture. There could be species that exist in isolated groups, and that if a foreign individual is accepted into the group, it is required to adopt the cultural norms of the group. In such a species, culture and cultural evolution are possible in the absence intergroup of diffusion. That said, diffusion of behavior is an indication of culture and should thus be understood not as a criterion for culture, but instead as evidence of culture.

Tradition is described as “patterns persist from innovator’s generation to the next one” (1992, p. 77). Like diffusion, tradition is a natural consequence of culture: culture spreads from individual to individual, and it is highly probable that many cultural variants will have models from an older generation. That said, is tradition in this transgenerational sense necessary for culture? The framework introduced above implies that culture can (and should) be defined independently of tradition in this sense. Some cultural variants could sweep through a generation, causing lasting changes in their behavior, but die out within that generation. In humans, we would not deny a particular fashion trend to be cultural just because nobody under thirty would be caught dead dawning it. Similarly, one could imagine species whose culture is always confined within a generation. Such a species may be improbable, but is not impossible. Thus tradition—as defined by McGrew—is an indicator of culture (since culture is almost always associated with traditions), not a necessary condition.

Non-subsistence is described as “pattern transcends subsistence” (1992, p. 77). This is a condition McGrew added so that culture is present in realms outside of subsistence. For chimpanzees, he offers an example of males from one cultural community tearing up leaves during courtship. Like many of the criteria offered by McGrew, I take this one to be empirically correlated with culture, but not a necessary condition for culture. A species could have all of its cultural variants be related to subsistence.

Naturalness is described as “pattern shown in absence of direct human influence” (1992, p. 77). The definition of culture offered above requires that the cultural information must flow through the behavior in bringing about culture in others. Thus, if humans change the environment of an animal, thereby changing its behavior, we should not regard this as culture. Although this is true, if a nonhuman animal learns a behavior from a human, but this animal goes on to serve as a model for conspecifics, the “artificial” behavior could become a cultural norm for the species.

In sum, the criteria offered by McGrew are, for the most part, *indicators* of culture as defined above. His intent was to offer empirically observable, measurable criteria and, as such, his list does a good job pointing to criteria that indicate culture. But these criteria, however, should not be understood as a constituting a *definition* of culture. If we ask *what is animal culture?* then the definition offered in the “What animal culture is” section is a good answer. But if we ask *what are reliable signs of culture?* then the criteria discussed in this section are a good answer.

Conclusions

The framework provided here accords well with standard practice in the science of animal culture. The common method of discovering behaviors that differ across ecologically similar geographic areas will pick out many cultural variants, though it will leave some undetected. Even if all human groups begin playing the banjo, banjo playing should still count as a cultural behavior. Similarly, it is possible for animal species to have cultural universals. Searching for behavioral differences not linked to environmental or genetic differences should thus be a starting point, not a decisive test. Instead, using the definition of culture elaborated above, we should ask whether the behavioral pattern is maintained by information transmitted via performances of the behavior in others.

The benefit of using the concept of culture here is that it will help us to be clear about what animal culture is and what it takes for a species to be cultural. And it allows us to keep clear about the difference between culture itself and the operational criteria one should use to search for and quantify culture. As we have seen, of the criteria offered by McGrew are, for the most part, reliable indicators of culture. In refining these criteria and developing new ones, one can use the definition offered here, asking the question of what observations can reliably indicate culture in this sense.

The conception of culture articulated here is inclusive—any species that uses information in the way described exhibits cultural behaviors. Despite this openness, the conception nevertheless does justice to much of what counts as culture in humans. Patterns of human behavior—languages, techniques, rituals, etc.—are maintained by culture. Some normative aspects of culture, or features linked to class (high vs. low culture), are not a part of culture as conceived here. But this is a strength, not a weakness, since it allows animals to be cultural in the purely informational sense, but also allows culture to be elaborated, supplemented, and transformed into the richly symbolic, normative world of humans.

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Further reading

K. N. Laland and B. G. Galef. *The question of animal culture* (Harvard University Press, 2009) offers an excellent collection of articles on culture in animals. G. Ramsey, “Culture in humans and other animals” *Biology & Philosophy* 28 (2013): 457-479 provides a more expansive discussion of animal culture than that found here. K. Laland and V. M. Janik, “The animal cultures debate” *Trends in Ecology & Evolution* 21 (2006): 542-547 offers an overview of recent debates about animal culture and suggests about how to weigh evidence about animal culture. E. Jablonka and M. J. Lamb, *Evolution in four dimensions, revised edition: Genetic, epigenetic, behavioral, and symbolic variation in the history of life* (MIT press, 2014) centers on human evolution, but proposes a general framework for understanding inheritance systems, including that of culture. Much work on cultural evolution, such as T. Lewens. *Cultural Evolution: Conceptual Challenges*, (Oxford University Press, 2015), A. Mesoudi. *Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences* (University of Chicago Press, 2011), and P. J. Richerson and R. Boyd. *Not by genes alone* (University of Chicago Press, 2004) is about human evolution, but these are also insightful for understanding culture in animals.