Making Space for Traditions

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For quite some time, the question of continuity across species with respect to culture has been linked in the academic world with definitional issues: What is culture, and how we can identify culture in a nonverbal species?[1–4] Behavioral scientists agree that behavioral traditions are that aspect of culture we can study in nonhuman animals, and we recognize that traditions are widespread in the animal kingdom (reviewed in Fragaszy and Perry,[5] see Laland and Hoppitt[6]). However, confirming candidate traditions in nonhuman primates has proven frustratingly difficult. The difficulties experienced in identifying and studying traditions in nonhuman primates are correctable because they arise more from a combination of poor logic and conceptual confusion than from an inability to collect appropriate data. I argue that explicit evidence concerning social learning is necessary to evaluate the status of a behavioral practice as a tradition, and I suggest some ways that such evidence can be collected in natural settings using correlational methods and longitudinal designs. Clearer understanding of the social basis of traditions in nonhuman animals is essential to make headway in understanding their relation to human culture. No matter what else one includes in a definition of culture, a social basis for its existence is axiomatic.

A DEFINITION OF TRADITION

A tradition is a behavioral practice that is shared among members of a group; is performed repeatedly over a period of time (that is, it is enduring); and depends to a measurable degree on social contributions to individual learning for its appearance in new practitioners (for elaboration see Fragaszy and Perry[7]). I will consider the implications of this definition for how we can identify traditions and how we should study them. At this point, I would like merely to point out that this definition does not address whether a behavior is unique to a group or varies across groups. Social contribution to the acquisition of the behavior by new practitioners is a requirement of a tradition; whereas variation of that behavior across groups is not.

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Key words: social learning, niche construction, process model, group comparison model, inductive reasoning

Evolutionary Anthropology 12:61–70 (2003)
DOI 10.1002/evan.10104

THE BIOLOGICAL SIGNIFICANCE OF TRADITIONS

The claim is often made that humans, through culture, are the only species whose behavior has effectively modified natural selection (for example, through agriculture or medicine). However, a human-centered perspective on the relation between culture and biological evolution is misleadingly narrow. Many species modify their environments through their behavior, a process labeled "niche construction" by Laland, Odling-Smee, and Feldman[8] (see also Odling-Smee, et al.[9]; Lewontin[10]). When the effects of niche construction remain local (and therefore can accumulate and persist) they can modify the environment for subsequent generations. A clear example of niche construction affecting humans has been described by Durham.[11] Human pastoralist groups are able to digest lactose and can eat dairy products and drink milk; human groups with other subsistence methods (for example, hunter-gatherers and agriculturalists) lack the appropriate digestive enzyme and are lactose-intolerant.

Niche construction in a very wide sense is potentially possible in all orders of living creatures, reflecting biological processes as varied as overt behavior (for example, beavers constructing their dams) to metabolic activity in microorganisms influencing the properties of the soil in which they live.[12] Niche construction is more likely, in evolutionary terms, to occur where its effects remain local, so that its benefits are available to the individuals paying the costs of producing the effects. Niche construction is therefore most likely to evolve in species with certain types of social systems and settlement patterns.[12] In mobile animals, niche-construction processes are more likely in species where individuals remain near one another or otherwise encounter the products of each other's activity on a regular basis. Social learning within groups (so that impact on the environment remain local) supports niche construction and enhances its feedback potential in natural selection. Behavioral traditions are one element of constructed niches; they are biologically significant for this fundamental reason. Alvard[13] makes the same point about human cultures, but it is important to recognize that this point applies to nonhuman species as well.

Traditions may support the maintenance of mundane but adaptive practices (such as using certain travel routes) among members of a living group. They may also result in the spread of a new practice. Both the continuation of familiar practices and the dissemination of new practices are biologically important, but behavioral innovations have generated more scientific interest among those who are interested in traditions. One reason for this bias is that investigators thought that we could evaluate the likelihood that a tradition is developing by examining the pattern of dissemination, or the "diffusion curve." This, however, is not the best reason to be interested in innovations. As Laland and Kendall[14] note, "It would certainly be terrific if social learning of a trait within a particular ecological context carried with it a signature pattern of diffusion that could be easily distinguished, and this would throw a new light on field data for the spread of innovations, such as potato washing in macaques. Unfortunately, this discussion has been carried out from a position of almost total ignorance of what patterns might be predicted if particular learning processes are operating. Most strikingly, there has been little consideration given as to what kind of diffusion curve might be expected when exclusively asocial learning processes are in operating in a population. . . . In our judgment reasoning as to the nature of the learning processes underlying the diffusion of an innovation on the basis of the shape of its diffusion curve is premature in the absence of a truly satisfactory body of theory that makes detailed predictions based on an extensive modeling of the relevant processes. The suggestion that asocial learning is likely to lead to linear increase over time and social learning to acceleratory or sigmoidal diffusion should now be regarded as discredited."

We may still be especially interested in the diffusion of innovations within social groups or populations because they provide a substantial fitness benefit (as using tools to open Neesia fruits may do for orangutans[15]) and because they afford an opportunity to watch individuals acquire a new practice, but we cannot evaluate the social contribution to the diffusion of a new behavior solely by the shape of the diffusion curve. We need to look more closely at the individuals that are performing the behaviors to make a determination about the contribution of social context to the diffusion of any behavior.

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WHAT IS SOCIAL LEARNING?

Traditions reflect social contributions to individual learning. In accord with the literature in this field, we use "social learning" to refer to the process in which social context contributes to skill development. We must recognize that social learning is defined by the context of learning, not by a distinctive process or a distinctive neural structure.[16] A more accurate but less convenient term for the phenomenon is "socially-biased learning." Hereafter I use these terms interchangeably. The field of animal behavior sports a large and growing literature on social learning. For example, the issue of Animal Behaviour that arrived as I was writing this article (June 2002; volume 63, number 6) contains four articles on social learning by rats, whales, song sparrows, and domestic chickens. It seems to me, social learning currently garners approximately as much attention from the animal behavior community as do the issues of mate choice, foraging strategy, or dispersal mechanisms.

Many contemporary treatments of social learning involve an implicit assumption that such learning occurs through the transfer of information from one individual to another. An alternative view, well represented in contemporary anthropology and psychology, considers cognition as the process of organizing and maintaining streams of activity.[17–20] In this view, activities of organisms are always grounded in ongoing engagement with the environment. All experience occurs in a background of meaning. That meaning is a composite of social as well as asocial elements and encompasses the current emotional and motivational state of the individual.[21] In this framework, there is no possibility to separate "social" from "asocial" learning in terms of the processes occurring within the individual. Rather, social and asocial learning differ in the external context in which learning occurs.[16,22] In this view, it is more useful to speak of social learning as influence on action than to speak of it as transmission of particulate, abstract, or representational knowledge from one individual to another. Social learning and traditions across species comes from the depth of meaning afforded by the social component of the environment, which affects the likelihood that individuals will generate similar practices from learning in the presence of others (see Matsuzawa and coworkers[23] for a convergent view). The particular mechanism of social influence is less important here than the likelihood that one individual affects the activity of another.[24]

How does this happen? A social partner alters the experience of the learner compared to experience without the social partner.[25] The trajectory of action and perception through time is different in social versus nonsocial conditions. This could arise because social partners generate particular experiences for others—they are animate, active agents, and they produce behaviors that are particularly salient to conspecifics. Learners may attend preferentially to conspecifics, and may be predisposed to respond in particular ways to particular "signals" the conspecifics generate or behaviors in which certain individuals engage. This notion seems relevant to many proposed mechanisms of social learning, including those grounded in information-processing language and those grounded in Pavlovian conditioning.[16,26,27] The added experimental aspect arising from social context can channel and scaffold individual efforts to acquire expertise. Social context constitutes a means of focusing behavior more effectively or differently than would have occurred in an asocial context.

Sometimes quantitative modelers make an assumption that socially biased learning is distinctive from individual learning in function or in response to natural selection, but this is merely a convenient assumption used to explore the evolutionary consequences of different organizations of learning.[28,29] There is no competition within the individual between reliance on social learning and reliance on individual learning; they are not different things. Social learning is merely learning that is influenced by social context.

Most often we think of traditions in nonhuman primates in relation to technical skills—foraging techniques, for example, as in the classic example of the Japanese macaques at Koshima starting to wash sweet potatoes in the ocean nearly fifty years ago.[30] But as Perry and Manson[31] and Laland and Hoppitt[6] point out, social learning can produce other kinds of traditions as well, and these also deserve our attention. For example, a broad definition of social learning encompasses one individual learning about the world from simply accompanying another. When a naïve individual accompanies its social group on travels through the home range, it can learn the locations of resources and habitual paths among them, as guppies (*Poecilia reticulata*) and French grunts (*Haemulon* sp., a coral-reef fish) do.[32–34] The behavior of the others allows (or even leads) the learner to generate experiences and encounter resources it would not otherwise. By so doing, the others enable the learner to learn ways of behaving, such as using particular paths from place to place, more quickly than it would learn on its own.

A broad definition of social learning also covers the acquisition of social skills that involve direct interaction with partners. Individuals can learn specific, and sometimes idiosyncratic modes of interacting with others (such as the conventional affiliative behaviors in white-faced capuchin monkeys described by Perry and Manson[31] and Perry and coworkers.[35]) When the behaviors acquired through direct interaction are typical of the species, we describe this learning process as socialization.[36] When the behaviors are idiosyncratic to a dyad or a group, we describe the process as conventionalization.[37] Some authors prefer to incorporate additional strictures to this very general definition, specifically to rule out as social learning the behavioral changes that accompany, for example, direct social interactions, such as displaying submission to a more dominant individual or coordinated sequences of social interaction during courtship.[38] Perhaps we will eventually develop phrases to distinguish these various settings for social learning—one to refer to social learning that is directly dependent on another's actions, but not interactive (that is, learning from demonstrations), another for social learning that is dependent on direct interaction between participants, and another for social learning arising through passive exposure merely from accompanying others. The broadest definition includes all the ways that animals can develop shared behaviors that depend in some way upon the social context for their repeated generation.

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A PROCESS MODEL OF TRADITION

Recall the definition of a tradition given earlier: a behavioral practice that is shared among members of a group, enduring, and depends to a measurable degree on social contributions to learning for its appearance in new practitioners. All three of these properties are scalar, not categorical. Prototypically, a tradition is shared among most or all members of a group (Tomasello's[39] dimension of universality), although it could be maintained by just one dyad or just one class of individuals (for example, members of one matriline or only juvenile females). The extent to which social influence affects the generation of shared practice can vary, however, and this definition does not specify what extent of shared practice reflects social influence. Similarly, how long a behavioral practice must persist to qualify as "enduring" is a matter of debate. Some theorists acknowledge ephemeral traditions (shared behavior practices lasting a few days to a few months) in humans as well as other species[3,6,8,31,35,40]; others restrict the term to behaviors that persist across generations.[2,41–43] In short, a shared practice can persist for days to the remainder of an individual's life, the shared behavior can be evident in as few as two individuals to an entire group, and the extent to which social influences affect the generation of the practice in new individuals can vary from minimally helpful to absolutely necessary.

In this view, traditions can vary along three orthogonal dimensions: duration, distribution, and extent of contribution of social influences to the expression of the behavior across individuals within a group. Traditions can thus be conceived as occurring within a "tradition space," as illustrated in Figure 1 and labeled the "process model," to emphasize that traditions are identified according to properties of behavior observed over time within a group. Here the three orthogonal dimensions are represented as *X*, *Y*, and *Z* axes. Now traditions can be seen as falling along a scale in each dimension. Behaviors that are long-lasting, are present in most or all members of a group, and are strongly dependent on social influences for their generation in new practitioners occupy one quadrant of this space (as in Panel A). Behaviors meeting these criteria fall clearly within the common meaning of the term "tradition." How far down or out from this space can we go and still identify a behavioral practice as "tradition"? To give three examples, what about behaviors that are relatively ephemeral but widespread and highly dependent on social influences—behaviors we might designate "fads" (depicted in Panel B)? Or behaviors that are long-lasting and widespread within a group, but are not strongly dependent on social influences (in other words, are often independently generated, as depicted in Panel C)? Or behaviors that are clearly dependent on social influences for their generation, but appear only in a few individuals within a group (depicted in Panel D)? Of these latter cases, can we call all three traditions? Do we need to subdivide this concept to do justice to these three dimensions? I think it is too soon to say.

ANOTHER MODEL OF "TRADITION SPACE" AND ITS PROBLEMS

The process model is at variance with the usual way field observers have approached the problem of identifying candidate traditions. Most discussions in the contemporary literature on traditions or culture in nonhuman animals, particularly primates, are grounded in a comparison of a completely different set of attributes, namely the degree of similarity of the behaviors seen in different social groups; the (usually hypothetical) degree of genetic and behavioral exchange among members of different groups; and the extent of environmental similarity across sites inhabited by different groups. I refer to this paradigm as the group-comparison model of traditions. The argument goes like this:

1. Group *X* and Group *Y* are currently or were until very recently members of a single breeding population (that is, "genetically similar").
2. Group *X* performs an action in one form and Group *Y* either does not perform it or performs it in a distinctively different form.
3. No obvious environmental difference limits the two groups from exhibiting the same form of the behavior.

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This model relies on characteristics unrelated to an essential feature of traditions. Their dependence on social context for acquisition by new practitioners of the behavior in question. However, this is the model that underlies, for example, the listing of behavioral variations as cultural traits in chimpanzees studied at different field sites published by a consortium of field observers[4,43] or the compendium of behavioral variations seen in cetaceans published by Rendell and Whitehead.[44] McGrew[2] suggests that field primatologists in particular adopt this approach because their subjects of study are too long-lived to adopt an ontogenetic, or process, approach. To be sure, all those interested in traditions are concerned with their social foundations. Still, many researchers accept the group-comparison model to some extent as a practical alternative to the process model.

The problem with the group-comparison approach is that comparisons of extant behaviors, no matter how different the behaviors appear across groups, no matter how similar the environments, or how similar in genetic makeup the populations, are never sufficient to resolve whether any behavior is traditional in a particular group. A tradition is not confirmed until one can show that social learning contributes to the generation of a practice in new practitioners. The group-comparison data only suggest that some behaviors are likely to be acquired in part through social learning. However, traditions are not limited to behaviors that vary across groups, and we may be seriously limiting our search by looking only at such behaviors.[15,45] Huffman and Hirata[46] illustrate the problem in their discussion of the repeated separate developments of stone-rubbing traditions observed in free-living groups of Japanese macaques living in isolation from one another.

The group-comparison model of traditions is illustrated in Figure 2 as a three-dimensional space, where the axes are degree of phylogenetic relatedness (genetic similarity), degree of behavioral similarity, and degree of environmental or ecological similarity. Here, the similarity between two or more groups is measured at one point in time or over an extended period. The small ball shows the ideal situation for identifying a candidate tradition according to this conception: Two groups are highly related phylogenetically (indeed, are members of a single breeding population) and inhabit similar microhabitats, but they vary distinctly in the form of behavior *X*. Often the behavior pattern is widely evident in each popu-

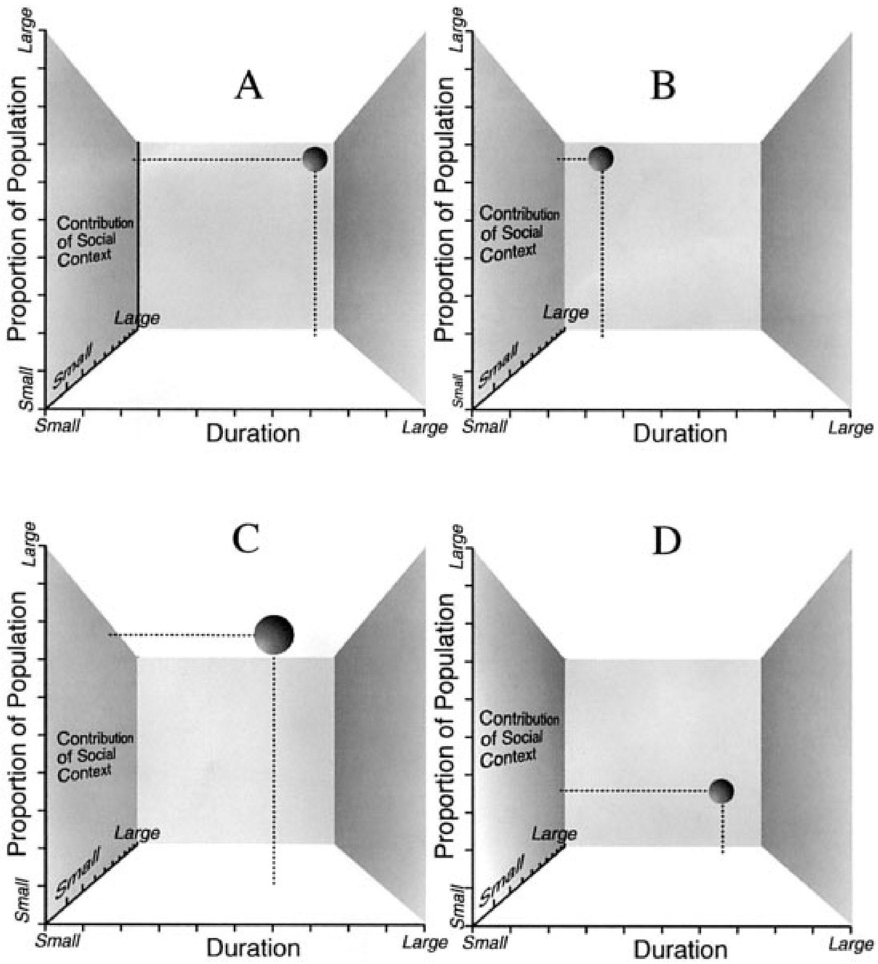

Figure 1. The process model of tradition conceived as a three-dimensional space. The defining axes are the duration of the behavior within the group (X axis), the proportion of the population displaying the behavior at any one time (Y axis), and the contribution of social context to the acquisition of the behavior by new practitioners (Z axis). Any distinctive behavior can, in principle, be placed in a unique location in this space. Panel A: A prototypical tradition which is a behavior that is long-enduring, evident in most members of the group, and largely dependent on social context for its acquisition. Panels B–D: More problematic cases, where the behavior is evident only for a short time (B), social context provides a measurable but small contribution to the generation of the practice (C), or only a small proportion of the population exhibits the behavior (D). Reprinted from Fragaszy and Perry (2003). Reprinted with permission of Cambridge University Press.

lation, and there is usually an attempt to verify longevity of the pattern. However, most often there is no evidence bearing on the ontogeny of the behavior in new practitioners. This model, however, does not get at the essence of what a tradition is—a behavior pattern shared among members of a group that depends to a measurable degree on social contributions to the generation of the behavior in new practitioners. The model identifies one possible outcome of the process, which is behavioral differences between groups. Unfortunately, other processes besides social learning can lead to the same outcome, and this model cannot discriminate between false positives (behavioral differences that are dependent on asocial factors and independent of socially aided learning) and true traditions. As noted, it is also prone to false negatives because it cannot identify behaviors that are dependent on socially aided learning but are similar across groups.

The large ball in Figure 2 illustrates a common and visibly problematic situation. In this case, groups are judged to be somewhat differentiated genetically, to live in somewhat varying habitats, and to exhibit some degree of behavioral variation. What can this model now predict about the likelihood that the variations between the groups in behavior *X* are supported by social learning? It cannot speak to this issue at all. It is important to note that drawing a conclusion from this model in this situation is no more problematic, on logical grounds, than drawing conclusions in what is considered the ideal situation, indicated by the small ball.

From a developmental (epigenetic) perspective, the group-comparison model suffers from the flawed assumption that genetic and environmental differences can replace social learning as explanations for observed differences. From an epigenetic point of view, these are independent levels of explanation.[47–49] Genetic and environmental circumstances surely affect behavior, and they do so by influencing development, not by acting outside of development. Positing genetic and environmental influences on behavior in no way removes the requirement for a developmental understanding of behavior. It simply acknowledges that development occurs within a particular context.

The group-comparison model suffers from additional flaws. Given that social learning may work together with the factors that the group-comparison model would consider plausible alternative factors (for example, ecological variation), this model works against confirmation that any behavior is a tradition (see Dewar[45] for elaboration of this problem). Moreover, this model does not provide insight into how a tradition is maintained or in what ways it is dynamic.[6,14,31] In short, the group-comparison model is afflicted by so many serious shortcomings of logic and scope that it is hard to find much in it worth retaining.

I believe that the inadequacies of the group-comparison model are partially responsible for the frustrations that many have expressed with the task of trying to confirm that behaviors of particular interest are or are not traditions, and the equal frustration of those who see claims of tradition as over-rated. As the model is logically inadequate, the claim for tradition that it can muster is necessarily weak. But is this unsatisfac-

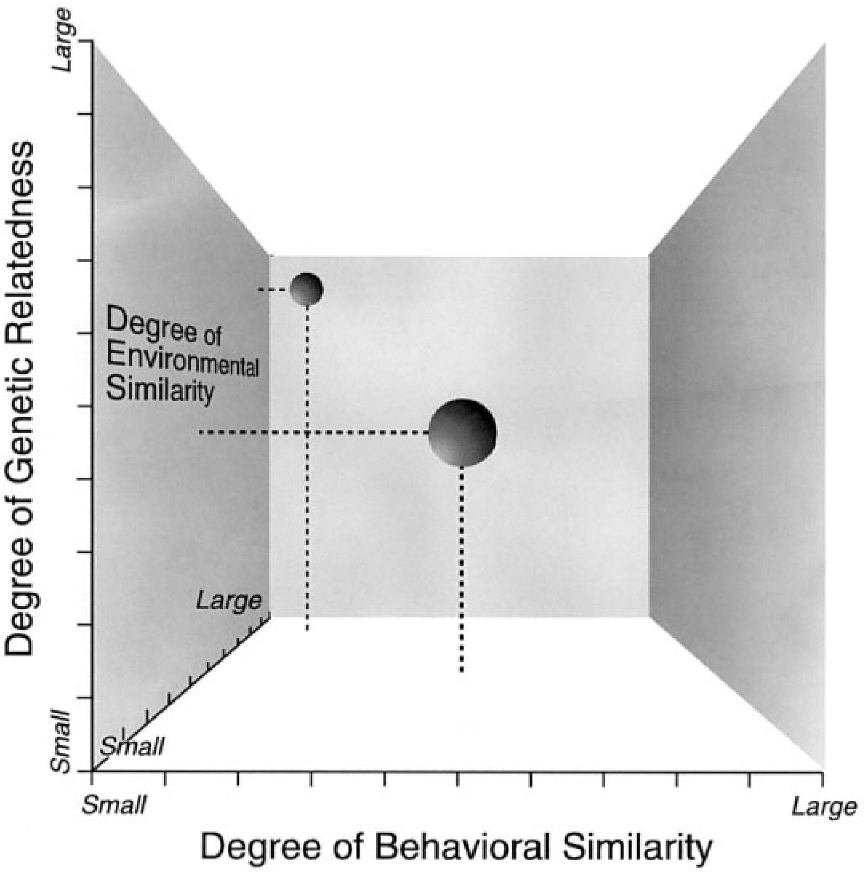

Figure 2. The group-comparison model of tradition conceived as a three-dimensional space. The location in space here defines the relation between two or more groups: the degree of similarity for the behavior of interest (X axis), the degree of genetic similarity for the groups under comparison (Y axis), and the degree of environmental similarity for the groups under comparison (Z axis). The small ball indicates a case that would be identified as a strong candidate for the label "traditional": A behavior that shows strong differences across genetically similar groups living in similar environments. The larger ball illustrates a more problematic case: A behavior that is moderately different in groups with moderately different gene pools and that live in moderately different environments. Reprinted from Fragaszy and Perry (2003). Reprinted with permission of Cambridge University Press.

tory state of affairs necessary? I don't believe so. The process model of traditions does not suffer from these flaws, and we can indeed collect evidence from both field and laboratory that can be addressed with that model. Next, I consider what kinds of evidence we should be collecting that can bear more deeply on the question of whether a particular behavior in a nonhuman species is a tradition and how it is acquired by new practitioners.

METHODS TO STUDY TRADITIONS

Causal Inference

John Stuart Mill[50] laid out four methods of inductive reasoning using comparative evidence: Agreement, Disagreement, Residues, and Concomitant Variation (summarized by MacLarnon[51]). The first two methods rest on the principles that by comparing two instances in which a phenomenon occurs and the comparison groups have only one element in *common* (Agreement) or comparing two instances in which a phenomenon occurs in one group but not in another and only one element is *different* between the comparison groups (Disagreement) we can conclude that a causal relationship, or an enabling relationship, exists between a certain condition and the phenomenon under study. The Method of Disagreement is the familiar logic of experimental design, where one independent variable is manipulated to determine its effect on one or more dependent variables, holding other independent variables constant. Combining these two methods produces the Joint Method of Agreement and Difference, wherein if both a set of dissimilar circumstances save one element *X* (Agreement) and a set of similar circumstances save the same element *X* (Disagreement) show the expected relation of presence and absence of phenomenon *P*, we can draw a strong conclusion about the necessity of element *X* to the occurrence of phenomenon *P*.

. . . field observers can document social contexts in which behaviors occur, changes over time in individual performance, and intragroup variation in behavior at a particular time; they also can seek comparable evidence about specific practices in other groups of the same species or related species. All of these kinds of evidence are useful to establish that social context aids a member of a group to acquire a behavior that others in the same group also perform.

Correlation

Phenomena in the natural world rarely lend themselves to the strict standards of evidence required by either the Methods of Agreement or Disagreement or their union (Joint Agreement and Disagreement) because the necessary experimental manipulations are rarely possible, and because multiple factors influence the occurrence of virtually all phenomena. Hence, the second two principles take on great importance for studies of naturally occurring phenomena. In these methods, we measure the magnitude of a phenomenon rather than its presence or absence.

In the Method of Residues (Mill's third method), one subtracts the magnitude of a phenomenon known to be associated with one set of conditions from its magnitude observed in a different, but closely related, set of conditions (ideally, similar conditions with one categorical difference). We attribute the difference, or residual, in the magnitude of the phenomenon to the differing conditions. For example, we may be interested in the frequency of grooming between groups that vary (ideally, only) with respect to the presence or absence of a particular kind of parasite.

The Method of Concomitant Variations (Mill's fourth method) similarly relies upon a comparison of the size of a phenomenon between two or more circumstances. In this method, one scales the magnitude of a particular relevant variable that varies in scalar fashion (say, risk of predation) with the magnitude of the phenomenon of interest (say, group size). In the case of the relationship between risk of predation and group size, the group is the unit of analysis. Van Schaik[15] uses this logic to evaluate the relationship between party size and the presence of putative traditions in chimpanzees. This method can also be used to evaluate the concordance between behavioral similarity in pairs of animals within a group, such as the use of a particular foraging technique, and some other aspect of their behavior with each other, such as the proportion of time they spend in proximity to one another, as illustrated in Panger and coworkers[52] (see also Perry and coworkers[35]). In this case, the pair is the unit of analysis.

Neither of these methods (Residues or Concomitant variation) provides the clear evidence of causal or conditional relationship that the first two methods do. Rather, they allow us to identify that a relationship exists between the degree of some condition between groups, or between dyads within a group, and the probability that the dyad shares a behavioral characteristic. One can imagine experimental designs with natural populations that could provide strong evidence of the necessity of social context for the perpetuation of a particular behavioral practice, as Laland and Hoppitt outline in this issue. Unfortunately, the designs involve wholesale removal and replacement of natural populations, and thus are unlikely to be carried out very often. One may prefer the methods of strong inference (the first two methods) because they support a stronger conclusion about causal necessity and sufficiency for a given variable. However, when these methods are not possible, it is better to use correlational methods correctly than to use experimental logic incorrectly.

Considering each new practitioner as a new link, and a series of links as a transmission chain, we can evaluate how rapidly new practitioners develop the behavior with differing forms of social support, how close the behavioral resemblance remains across links, and how different the patterns are in different social units. This task is easier if the behavior is present in some groups and not others, . . .

What evidence for social learning can we expect to collect from naturalistic observations? It is not possible to obtain the same evidence that we can obtain in experimental situations. Field observers cannot train an individual to serve as a demonstrator to others, nor can they group animals by skill levels on a given task. Observers of animals in natural settings cannot determine with certainty that the changes in behavior they observe across time in an individual's proficiency or form at some particular task reflect social influence on learning because they cannot rule out asocial influences by comparison with a set of individuals who encounter the task while alone (a control group). Nevertheless, field observers can document social contexts in which behaviors occur, changes over time in individual performance, and intragroup variation in behavior at a particular time; they also can seek comparable evidence about specific practices in other groups of the same species or related species. All of these kinds of evidence are useful to establish that social context aids a member of a group to acquire a behavior that others in the same group also perform.

Longitudinal Methods

The comparisons envisioned by Mills[50] to identify the contributions of some condition to the occurrence of a phenomenon do not exhaust our analytical strategies, however. We have an arsenal of other methods that support analysis of development. Developmental analyses concern *how* a characteristic comes about or changes through time in an individual and in groups. Longitudinal data relevant to understanding the origins of traditions in nonhuman animals come from studies of vocal learning in many taxa, but especially in birds.[53,54] The now-classic developmental studies of Terkel[55] demonstrating the development of pine-cone stripping by young black rats whose mothers use this method of feeding are excellent examples. Mann and Sargeant[56] provide longitudinal data for convergent feeding techniques by mother and daughter bottlenose dolphins. In nonhuman primates, the best examples of developmental studies relevant to understanding the origins of shared practices are those of stone handling by

Japanese macaques,[46,57] the development of nut-cracking by young chimpanzees,[58] and the development of various feeding techniques by young orangutans.[59]

Examining Appropriate Hypotheses

Sometimes those conducting naturalistic observations argue that demonstrating the necessity of social learning in the generation of similar behaviors in different individuals requires ruling out all plausible alternative explanations (usually, environmental sources, such as resource availability, and presumed genetic differences).[2,60] Unfortunately, it is a logical impossibility to rule out all other mechanisms besides social learning that might produce similar behaviors in two or more individuals on the basis of observations of spontaneous behavior in natural settings. Field observations simply cannot provide the data necessary for such strong inferences. This is a misguided attempt to use the logic of the Method of Agreement when the elements needed to use this logic are not available (see Dewar[45] for a similar argument). It is logically possible, however, to adopt the Method of Residues or of Concomitant Variations and to show that social learning aids the generation of similar behaviors. This can be done, for example, by documenting the development of skill as a function of the extent of social support during learning (correlating rate of skill development in several individuals with extent of social support). To confirm that social learning aids in the generation of similar behaviors, we need to document the spread of a specific behavior to multiple new practitioners in a variety of circumstances. Considering each new practitioner as a new link, and a series of links as a transmission chain, we can evaluate how rapidly new practitioners develop the behavior with differing forms of social support, how close the behavioral resemblance remains across links, and how different the patterns are in different social units. This task is easier if the behavior is present in some groups and not others, and logically even easier if a behavioral innovation is observed at the outset and its spread followed within a group. It is still possible, however, even if the behavior is present in all groups.

Persistence

Some authors emphasize the persistence of a behavioral pattern across biological generations as necessary to accord it the status of a tradition.[2,43] As may be surmised from the "traditions space" model provided in Figure 1 and discussed earlier, I find this requirement too restrictive. Traditions that endure across generations allow one generation to influence the conditions of natural selection of the next generation; the selective environment is scaffolded for the next generation by the behavior of the previous one, and thus traditions can have effects on fitness. However, in theory, even ephemeral traditions (lasting only a portion of the individual's life span) can have fitness consequences. Vocal traditions in many taxa drift in less than a life span; degree of adherence to the traditional song of the moment can still influence a singer's appeal to the opposite sex, and therefore the individual's fitness. As Perry and Manson[31] argue, there are theoretical reasons why social conventions indicating affiliation between members of a dyad in general should have short durations.

Genetic and environmental circumstances surely affect behavior, and they do so by influencing development, not by acting outside of development. Positing genetic and environmental influences on behavior in no way removes the requirement for a developmental understanding of behavior. It simply acknowledges that development occurs within a particular context.

In any case, identifying the frequency and distribution of a behavior in any population or set of populations at one point in time or over time *cannot* inform us of the contribution of social influences to the generation of that behavior. We need to learn whether social context aids in the generation of the shared behavior to evaluate a candidate tradition. This may seem difficult to achieve in natural settings, but the situation is far from hopeless. There are many different forms of evidence that can elucidate the critical third dimension in traditions, that of social contributions to the generation of the behavior in new practitioners.

CONCLUSION

I have proposed that we can conceptualize traditions as behaviors located within a specific region of the three-dimensional space defined by the axes of temporal duration, proportion of population displaying the practice, and contribution of social influences on the generation of new practitioners (the process model of traditions space; see Figure 1). The heuristic process model makes it clear why documenting group specificity and long (even intergenerational) duration of a behavior, currently the most frequently used data to argue for or against the status of a behavior as traditional in a particular group, will never be sufficient to make a strong claim for that status. The third dimension, contribution of social influence, must be examined in its own right; it is neither derivative of, nor predicted by, the other two dimensions. We do not yet have a principled basis to specify numerical values defining the area of traditions; that awaits further theoretical developments. However, the process model of traditions nudges us to look for ways to measure the effects of social influence on acquisition to achieve adequate definitional rigor for the phenomenon. This task is important no matter what level of explanation is under consideration. Field observations can illuminate traditions by documenting behavioral variation within groups in conjunction with patterns of social affiliations or (a less powerful method) across sites and the generation of skilled practice by new practitioners. Longitudinal data relevant to acquisition will enable us to identify traditions more rigorously than has been the case previously. Contemporary researchers are developing new ways of doing these things in studies of nonhuman primates.[5,31] Avian researchers have been doing this for some time.[53]

The take-home message is simply this: Clear concepts and sound logic will support vigorous study of traditions in nonhuman animals, and vigorous study of traditions in nonhuman animals can contribute to a biologically meaningful understanding of culture. I hope that the process model espoused here (see also Fragaszy and Perry[5]) is a step in this direction.

ACKNOWLEDGMENTS

I thank Susan Perry for many discussions about comparison and process models of traditions, and Charles Janson for helpful comments on a previous version of this article. Portions of this article are drawn from Fragaszy and Perry.[7]

REFERENCES

1 McGrew WC. 1992. Chimpanzee material culture: implications for human evolution. Cambridge: Cambridge University Press.

2 McGrew WC. 1998. Culture in nonhuman primates? Ann Rev Anthropol 27:301–328.

3 Boesch C, Tomasello M. 1998. Chimpanzee and human cultures. Curr Anthropol 39:91–604.

4 Whiten A, Goodall J, McGrew W, Nishida T, Reynolds V, Sugiyama Y, Tutin C, Wrangham R, Boesch C. 2001. Charting cultural variation in chimpanzees. Behaviour 138:1481–1516.

5 Fragaszy D, Perry S. 2003. The biology of traditions: models and evidence. Cambridge: Cambridge University Press.

6 Laland KN, Hoppitt W. 2003. Do animals have culture? Evol Anthropol 12. In press.

7 Fragaszy D, Perry S. 2003. Towards a biology of traditions. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 1–32.

8 Laland K, Odling-Smee J, Feldman M. 2000. Niche construction, biological evolution, and cultural change. Behav Brain Sci 23:131–146.

9 Odling-Smee F, Laland K, Feldman M. 1996. Niche construction. Am Nat 147:641–648.

10 Lewontin R. 1978. Adaptation. Sci Am 239: 156–169.

11 Durham W. 1991. Coevolution: genes, culture, and human diversity. Stanford: Stanford University Press.

12 Pulliam R. 2000 (November). Gaia, evolution, and the theory of niche construction. Colloquium presented to the Institute of Ecology, University of Georgia, Athens, GA.

13 Alvard M. 2003. The adaptive nature of culture. Evol Anthropol 12. In press.

14 Laland KN, Kendall JR. 2003. What the models say about social learning. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 33–55.

15 van Schaik C. 2003. Local traditions in orangutans and chimpanzees: social learning and social tolerance. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 297–328.

16 Fragaszy D, Visalberghi E. 2001. Recognizing a swan: socially-biased learning. Psychologia 44: 82–98.

17 Johnson, C. 2001. Distributed primate cognition. A review. *Animal Cognition.*

18 Thelen E, Smith L. 1994. A dynamic systems approach to the development of cognition and action. Cambridge: MIT Press.

19 van Gelder T. 1998. The dynamical hypothesis in cognitive science. Behav Brain Sci 21:615–665.

20 Reed ES. 1996. Encountering the world. New York: Oxford University Press.

21 Damasio A. 1994. Descartes' error: emotion, reason, and the human brain. New York: Putnam.

22 Ingold T. 1998. Commentary on Boesch and Tomasello: chimpanzee and human cultures. Curr Anthropol 39:605–606.

23 Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G. 2001. Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T, editor. Primate origins of human cognition and behavior. Tokyo: Springer Verlag. p 557–574.

24 Coussi-Korbel S, Fragaszy DM. 1995. On the relation between social dynamics and social learning. Anim Behav 50:1441–1453.

25 Russon A. 1997. Exploiting the expertise of others. In: Byrne R, Whiten A, editors. Machiavellian intelligence II: extensions and evaluations. Cambridge: Cambridge University Press. p 174–206.

26 Byrne. 1999. Imitation without intentionality: using string parsing to copy the organization of behavior. Anim Cogn 2:63–72.

27 Domjan M, Cusato B, Villarreal R. 2000. Pavlovian feed-forward mechanisms in the control of social behavior. Behav Brain Sci 23:235–249.

28 Laland K, Richerson P, Boyd R. 1996. Developing a theory of animal social learning. In: Heyes C, Galef BG Jr., editors. Social learning in animals: the roots of culture. New York: Academic Press. p 129–154.

29 Richerson PJ, Boyd R. 2000. Climate, culture and the evolution of cognition. In: Heyes C, Huber L, editors. The evolution of cognition. Cambridge: MIT Press. p 329–346.

30 Kawai M. 1965. Newly-acquired pre-cultural behavior of a natural troop of Japanese monkeys on Koshima Island. Primates 6:1–30.

31 Perry S, Manson JH. 2003. Traditions in monkeys. Evol Anthropol 12:71–81.

32 Laland K, Williams K. 1997. Shoaling generates social learning of foraging information in guppies. Anim Behav 53:1161–1169.

33 Laland K, Williams K. 1998. Social transmission of maladaptive information in the guppy. Behav Ecol 9:493–499.

34 Helfman G, Shultz E. 1984. Social transmission of behavioural traditions in a coral reef fish. Anim Behav 32:379–384.

35 Perry S, Panger M, Rose L, Baker M, Gros-Louis J, Jack K, MacKinnon K, Manson J, Fedigan L, Pyle K. 2003. Traditions in wild white-faced capuchin monkeys. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 391–425.

36 Box H. 1984. Primate behaviour and social ecology. London: Chapman and Hall.

37 Tomasello M. 1990. Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: Parker S, Gibson K, editors. "Language" and intelligence in monkeys and apes. Cambridge: Cambridge University Press. p 274–311.

38 Galef BG. 1988. Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In: Zentall T, Galef BG Jr., editors. Social learning: psychological and biological perspectives. Hillsdale, NJ: Erlbaum. p 3–28.

39 Tomasello M. 1994. The question of chimpanzee culture. In: Wrangham R, McGrew W, de Waal F, Heltne P, editors. Chimpanzee cultures. Cambridge: Harvard University Press. p 301–317.

40 Bikhchandani S, Hirshlifer D, Welch I. 1998. Learning from the behavior of others: conformity, fads, and informational cascades. J Econ Perspect 12:151–170.

41 Heyes C. 1993. Imitation, culture and cognition. Anim Behav 46:999–1010.

42 Sugiyama Y. 1993. Local variation of tools and tool use among wild chimpanzee populations. In: Berthelet A, Charaillon J, editors. The use of tools by human and nonhuman primates. New York: Oxford University Press. p 175–187.

43 Whiten A, Goodall J, McGrew W, Nishida T, Reynolds V, Sugiyama Y, Tutin C, Wrangham R, Boesch C. 1999. Cultures in chimpanzees. Nature 399:682–685.

44 Rendell L, Whitehead H. 2001. Culture in whales and dolphins. Behav Brain Sci 24:309–382.

45 Dewar G. 2003. The cue reliability approach to social transmission: designing tests for adaptive traditions. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 127–158.

46 Huffman M, Hirata S. 2003. Biological and ecological foundations of primate behavioral tradition. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 267–296.

47 Lehrman D. 1970. Semantic and conceptual issues in the nature-nurture problem. In: Aronson L, Tobach E, Lehrman D, Rosenblatt J, editors. Development and evolution of behavior. San Francisco: Freeman Press. p 17–52.

48 Gottlieb G. 1992. Individual development and evolution: the genesis of novel behavior. New York: Oxford University Press.

49 Michel G, Moore C. 1996. Developmental psychobiology. Cambridge: MIT Press.

50 Mill JS. 1872/1967. A system of logic: ratiocinative and inductive; being a connected view of the principles of evidence and the methods of scientific investigation. London: Longman.

51 MacLarnon A. 1999. The comparative method: principles and illustrations from primate socioecology. In: Lee PC, editor. Comparative primate socioecology. Cambridge: Cambridge University Press. p 5–22.

52 Panger M, et al. n.d. Variation in foraging patterns across capuchin groups. Am J Phys Anthropol. In press.

53 Janik V, Slater P. 2003. Avian and mammalian vocal traditions. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 213–235.

54 Catchpole C, Slater P. 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.

55 Terkel J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG Jr., editors. Social learning in animals: the roots of culture. San Diego: Academic Press. p 267–286.

56 Mann J, Sargeant B. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops aduncus*). In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 236–266.

57 Huffman MA. 1996. Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In: Heyes C, Galef G, editors. Social learning in animals. The roots of culture. New York: Academic Press. p 267–289.

58 Inoue-Nakamura N, Matsuzawa T. 1997. Development of stone tool use by wild chimpanzees. J Comp Psychol 111:159–173.

59 Russon A. 2003. Developmental perspectives on great ape traditions. In: Fragaszy D, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press. p 329–364.

60 Boesch C. 1996. Three approaches for assessing chimpanzee culture. In: Russon A, Bard K, Parker S, editors. Reaching into thought. Cambridge: Cambridge University Press. p 404–429.

Books Received

- Schrire, C. (2002) Tigers in Africa. vi + 58 pp. Cape Town: University of Virginia and University of Cape Town Press. 0-8139-2129-5 (paper) $12.50.
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- Boesch, C., Hohmann, G. and Marchant, L.F. (eds.) (2002) Behavioural Diversity in Chimpanzees and Bonobos. x + 285 pp. New York: Cambridge University Press. ISBN 0-521-00613-9 (paper) $33.00.
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