

Towards a biology of traditions

1.1 Introduction

One who sees things from the beginning will have the finest view of them

ATTRIBUTED TO ARISTOTLE

In late 1997, a series of exchanges occurred on the internet bulletin board established by Linda Fedigan a year earlier to facilitate communication among the select circle of individuals studying capuchin monkeys (genus *Cebus*, in the family Cebidae of the New World monkeys). Someone posted a description of a strikingly odd behavior she had noticed in her main study group of about two dozen white-faced capuchin monkeys (*C. capucinus*). The behavior, a pattern of two individuals interacting in an apparently affiliative manner, had not been described in the literature for any other animal species. Several members of the group performed this behavior with each other routinely over a period of seven years, and it appeared a perfectly familiar aspect of their social behavior that field season, as if they always did this odd thing (see Ch. 14, for more details about the mystery behavior). Nevertheless, they had not done this during the first year of the study, nor had she observed the behavior in the neighboring group. The researcher was understandably curious whether anyone else had ever seen anything like it, or had any ideas on how it might have originated or its function. A flurry of messages ensued over the next few weeks, with several researchers confirming the first person's suspicion that this behavior was not a universal behavior in white-faced capuchins, and not known at all in other species of capuchins. These respondents, moreover, provided their own examples of odd social behaviors common in their

groups, which they had assumed were present in other groups but were now wondering if that assumption were premature. At the conclusion of the on-line discussion, the correspondents were left with a tantalizing list of potentially group-unique behaviors in the genus, and the distinct impression that some of these might be traditions. As those who work with capuchins, including the two authors of this chapter, are firmly convinced that these monkeys are socially responsive as well as brash and intrepid individuals, we were all intrigued by the possibility that these monkeys might have behavioral traditions. To make such a claim publicly, and to place the phenomenon into the biological framework we were convinced was necessary, was obviously going to be a substantial project requiring the ideas and efforts of many people.

1.2 More than a question of culture

Behavioral scientists have often considered social learning in nonhuman animals as a precursor of culture as we know it in humans (e.g., Bonner, 1980). Culture has many meanings in anthropology, including belief systems, codes of conduct, and so forth, that we do not expect to exist in nonhuman species. The only essential element of human culture potentially shared with nonhuman species is the continuation of behavioral practices across generations through social learning. Although anthropologists generally agree that sharing this single domain with humans is not a sufficient basis to attribute culture to nonhuman animals (cf. Boesch and Tomasello, 1998; McGrew, 1992, 1998), the convergence still fascinates behavioral biologists. Early contributions suggesting a parallel between traditions in nonhuman animals and human culture were provided by Japanese zoologists conducting many of the first longitudinal observational studies of monkeys in natural conditions (Itani and Nishimura, 1973; Kawai, 1965; Kawamura, 1965; also see de Waal, 2001 for an overview). These researchers were very interested in the appearance of novel behaviors in groups of monkeys and the fact that other individuals eventually displayed behaviors that initially had been the province of a single “inventor”. Their term for the phenomenon was translated from Japanese into English as “protocultural”, “pre-cultural”, and “sub-cultural”; and the debate was on. A vigorous controversy has brewed ever since over what is necessary for a behavior pattern shared among members of a group to be identified as “cultural”, which species might be said to “have culture”, and which learning mechanisms are necessary to claim that a particular practice qualifies as “cultural”. Discussions of social learning in

nonhuman primates, and particularly chimpanzees, have been at the forefront of these controversies. The rate of discussion has now reached a feverish pitch. A sampling of titles of publications in the last four years alone at the time we are writing include, for example, “Cultural primatology comes of age” (de Waal, 1999), “Cultures in chimpanzees” (Whiten *et al.*, 1999), “Charting cultural variation in chimpanzees” (Whiten *et al.*, 2001), “Chimpanzee and human cultures” (Boesch and Tomasello, 1998), “Chimps in the wild show stirrings of culture” (Vogel, 1999), “Culture in nonhuman primates?” (McGrew, 1998), “Emergence of culture in wild chimpanzees: education by master-apprenticeship” (Matsuzawa *et al.*, 2001), “Primate culture and social learning” (Whiten, 2000), and “Orangutan cultures and the evolution of material culture” (van Schaik *et al.*, 2003). The *New York Times Magazine* issue on 9 December 2001, in an article entitled “The year in ideas”, included an essay “Apes have culture too”. In part, this torrent of interest is motivated by the concern that apes are losing the battle for survival in nature; the call is out to prevent “culturecide” as populations are decimated by human activities in their home areas. In part it is because we are just coming to realize things about apes that bring them ever closer, behaviorally, to the threshold that many have set dividing humans from nonhuman relatives.

This debate, regardless of its origins or purpose, is driven largely by anthropocentric, not biological, concerns about the meanings of culture. These anthropocentric concerns are outside the scope of our efforts here. Rather, we are interested in traditions as features of behavior in nonhuman animals without regard to whether these traditions meet any particular set of criteria for nomination as “cultural”. We define traditions as enduring behavior patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group. If there were another, less value-laden, term than traditions to describe such behavioral phenomena we would use that term. However, we do not have an alternative term at our disposal without creating a new word that would not be understood outside of our own small readership. So long as the term “tradition” captures best those aspects of shared practice that we are interested in here, we shall continue to use this term.

Arguments in favor of according a special status to primates in regard to social learning, and the probability that shared behaviors reflect social influences on learning (i.e., that primates have traditions), are often rooted in a simple notion of phylogenetic association. This notion is that species that share a more recent link with human ancestors in

evolutionary history are likely to share with humans more elaborated social learning. Alternatively, social learning might be more important in the lives of members of these species. However, phylogenetic association with humans is not predictive of social learning propensities (Box and Gibson, 1999; Fragaszy and Visalbergi, 1996). No distinctive form of social learning is unique to humans, or to humans and closely related primates (Russon *et al.*, 1998; see also Fritz and Kotrschal, 1999; Voelkl and Huber, 2000; Zentall, Sutton, and Sherburne, 1996). This strong statement applies even to "true imitation", according to Russon *et al.* (1998). Social learning in many forms is apparently widespread in the animal kingdom, although we have not looked for it intensively in many species. Box and Gibson (1999) urge us to look widely for possible cases of social learning in natural settings; many of the chapters in their book suggest why we should look for social learning in a variety of mammalian taxa where previously few had thought to look for such evidence. Social learning must be examined as an element in the behavioral biology of animals, rather than as a lead-up to, or incomplete version of, a (possibly) uniquely human characteristic (Box and Gibson, 1999; de Waal, 2001; Giraldeau, 1997; Avatal and Jablonski, 2000; Laland *et al.*, 2000).

Phylogenetic trends in the size and organization of the nervous system are useful supports for theories about behavioral evolution. For example, birds that store and retrieve thousands of nuts have an enlarged hippocampus, a part of the brain involved in memory formation, compared with closely related nonstoring species (Basil *et al.*, 1996; Krebs *et al.*, 1989). Relative forebrain size and absolute forebrain size both correlate positively with the number of reported instances of social learning and of behavioral innovations across taxa in nonhuman primates (see Reader, this volume; Reader and Laland, 2001). Similarly, the corresponding variable in birds (the relative size of the neostriatum and hyperstriatum ventrale) correlates positively with the frequency of reported feeding innovations across taxa (Lefebvre *et al.*, 1997), although evidently not to social learning or foraging habits (Ch. 4). Covariance between brain size and propensity to innovate and (in primates) to develop traditions would suggest that social learning is part of a functionally seamless whole reflecting overall neural power in a general sense, rather than specialized capacities for social learning or for innovation. This conclusion makes good sense if social learning is understood as modulation of learning through social context, as we argue below, rather than as a set of specific learning abilities. Big brains afford more modulated learning.

The extraordinarily conservative patterns of neurogenesis across broad taxonomic mammalian groups (Finlay, Darlington, and Nicastro, 2001) lead to the powerful conclusion that brains and behavior co-evolved in a most general way, rather than in accord with selective pressures for specific behavioral attributes (such as enhanced social learning propensities or propensities to innovate). In this view, we should expect behavioral flexibility and social sophistication in many forms in any species with relatively large brains, regardless of their membership in any particular taxonomic order. If Finlay *et al.* (2001) are correct that the size of all parts of the brain reflect conservative growth patterns, virtually always independent of specific selective pressures, then we should expect behavioral flexibility (afforded by a large isocortex) to be enhanced even in taxa where we cannot identify any particular selective pressure for a certain form of flexibility. In other words, capacities supporting social learning, like all forms of learning, may simply come along with brain size. What use specific taxa make of these abilities is likely to vary in accord with a constellation of ecological and social variables. This is our concern in this volume. What contributions to behavioral biology and to evolution might traditions confer on those taxa where they occur, and where might traditions occur?

1.3 The biological significance of traditions

Our particular concern in this volume is with traditions as one outcome of social learning. 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. Species modify their environments through their behavior, a process labeled "niche construction" by Laland *et al.* (2000; see also Lewontin, 1978; Odling-Smee, Laland, and Feldman, 1996). One consequence of niche construction is that behavior is conceptualized as more than the target of natural selection. It also modifies the environment for subsequent generations, so that now behavior is conceptualized as participating in the process of selection. As Laland *et al.* (2000 p. 135) put it, the evolutionary significance of niche construction rests on the feedback that it generates: "In the presence of niche construction, adaptation ceases to be a one-way process, exclusively a response to environmentally imposed problems: instead, it becomes a two-way process, with populations of organisms setting as well as solving problems."

One outcome of niche construction can be a shift in the genetic make-up of a population. A clear example of niche construction affecting regional genetic characteristics has been described by Durham (1991): human pastoralist groups are able to digest lactose and can eat dairy products and drink milk; human groups with other subsistence methods (e.g., hunter-gatherers, 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 (e.g., beavers constructing dams) to metabolic activity in microorganisms impacting the properties of the soil in which they live (Pulliam, 2000). Pulliam has modeled the consequences for microorganisms of altering their chemical surroundings, assuming two character types for the organism (constructors and nonconstructors). These models show that where niche construction occurs, niche constructors will come to dominate the population over a range of cost scenarios (where costs are incurred by the presence of nonconstructors). In other words, self-constructed ecosystems can over time come to be dominated by self-maintaining, mutualistic constructors. In this way, niche-construction processes can provide a benefit for all members of a community and can support multilevel selection as Sober and Wilson (1998) envision it occurs. Pulliam (2000) suggested that niche construction is an important feature driving the evolution of species assemblages (communities) dominated by mutualistic constructors, as observed in mutualistic communities of microorganisms living in the soil, for example.

Niche construction is more likely, in evolutionary terms, where its effects remain local, so that the benefits of niche construction 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 system and settlement pattern or in certain environments where movement is slow (Pulliam, 2000). 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 (which occurs within groups, so that its impacts on the environment remain local for that group) is clearly one mechanism supporting niche construction and enhancing its feedback potential in natural selection. Niche construction may produce "key innovations" that enable a species to make use of a resource which it previously could not use.

Behavioral traditions are one element of constructed niches; they are biologically significant for this fundamental reason. 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 specific innovation, for example a new method of processing food, inclusion of a new item in the diet, or a new means of regulating temperature or constructing shelter. Both the continuation of familiar practices and the dissemination of new practices are biologically important, but the key role of behavioral innovation in speciation has generated more interest recently on the part of (quantitative) evolutionary modelers. Most contributors to this volume are concerned to a greater or lesser degree with the role of social learning in generating new traditions; founded on a behavioral innovation that appears rarely in the population; two chapters in this volume (Chs. 3 and 4) address this issue primarily.

Several other contributions in this volume concern the evidence for traditions in various mammalian taxa, and what the behaviors in question contribute to the ecology of the groups where they are found. To most biologists, the controversies over whether or not an individual, population, or species exhibits "culture" are of no concern, but the possibility that traditions impact behavioral ecology, fitness, and evolution is of riveting interest.

We consider social learning and traditions from the perspective of ethology. Ethology is that part of biology most directly concerned with behavior. Ethology was established as a distinct branch of biology in the early years of the twentieth century and has matured into a vigorous field in the intervening century. As laid out by Tinbergen (1963), ethology is concerned with questions about behavior cast broadly in terms of causation (mechanism), ontogeny, evolution (phylogenetic history), and survival value (adaptive function). Since Tinbergen's (1963) seminal statement framing the scope of ethology, scientists studying the behavior of animals have recognized multiple levels of explanation as necessary for a comprehensive biological understanding of any behavior. Moreover, explanations at one level must be compatible with explanations at other levels: the organism is an integrated whole, with an unbroken connection to its individual and phylogenetic past and to its current circumstances. The power of this integrative perspective is evident in the contemporary vigor of ethology and its ability to interface substantively with other areas of biology (Kamil, 1998). We believe that explicitly treating social learning from this perspective will aid us in producing coordinated,

complementary data across field and laboratory projects that will speak powerfully to contemporary questions about social learning in all animals, including humans.

1.4 Definitions of social learning

Behavioral scientists define social learning, in its broadest meaning, as changes in the behavior of one individual that result, in part, from paying attention to the behavior of another (Box, 1984). A broad definition of social learning encompasses one individual learning about the world from simply accompanying another. For example, 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*) do (Laland and Williams, 1997, 1998). In this example, the behavior of the others allows the "learner" to generate experiences and encounter resources it would not otherwise; the others have by their behavior enabled the learner to learn.

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 affiliative behaviors of the kind described in Ch. 14). When the behaviors acquired through direct interaction are typical of the species, we describe this learning process as socialization (Box, 1984). When the behaviors are idiosyncratic to a dyad or a group, we describe the process as conventionalization (Tomasello, 1990). Some authors prefer to incorporate additional strictures to this very general definition, specifically to exclude 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) as social learning (Galef, 1988). 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 (i.e., learning from demonstrations); another for social learning that is dependent on direct interaction between participants; and yet another for social learning arising through passive exposure merely from accompanying others. For our purposes in this book, we accept the broadest definition, in accord with our interest in all the ways that animals can develop shared behaviors that depend in some way upon the social context for their repeated generation.

Some theorists challenge the notion, sometimes implicit but more often explicit in most contemporary treatments of social learning, that social learning occurs through the "transfer" of "information" from one individual to another. Information, after all, is not a thing. Learning does not entail the transfer of particles of information, unchanged during transfer across the space between heads (Ingold, 1998). An alternative view, well represented in contemporary anthropology and psychology, considers cognition as the process of organizing and maintaining streams of activity rather than the process of managing particles of knowledge (e.g., Gibson, 1966, 1986; Johnson, 1987; Reed, 1996; Thelen and Smith, 1994; van Gelder, 1998). In this view, activities of organisms are always grounded in ongoing engagement with the environment. All experience occurs in a background of meaning, and that meaning is a composite of social as well as social elements, and encompasses the current emotional and motivational state of the individual (D'Amasio, 1994). Knowledge and practice (behavior) are inseparable. Consequently, knowledge *per se* cannot be "transferred". Rather, an individual is continuously seeking meaning in others' perceived activities as well as all aspects of its own engagement with the current environment, and it alters its own behavior in accord with ongoing experience. In this framework, there is no possibility to separate "social" from "asocial" learning, or to consider learning processes as distinctive to one or the other (Frigaszy and Visalberghi, 2001; Ingold, 1998). What is distinctive about individuals acting in social settings is that they can generate behaviors that are similar to one another. The social learning process of concern to us is one of generation, not transmission. Adopting this perspective, what distinguishes social learning and traditions across species derives from the depth of meaning afforded by the social component of the environment, and the likelihood of generating similar practices (see Matsuzawa *et al.* (2001) for a convergent view).

Russon (1997) has suggested a similar interpretation of social learning in terms that are perhaps more familiar to biologists. In Russon's wording, a social partner alters the experience of the learner compared with experience without the social partner. The trajectory of action and perception through time is different in social versus nonsocial conditions. This could arise through increased salience of experiences that occur in presence of others, for example. Social partners generate particular experiences: 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 (Byrne, 1999; Domjan *et al.*, 2000; Frigaszy, 2000; Frigaszy and Visalberghi, 2001; Russon, 1999). Here we note that social context is a rich and ever-changing background for individual activity. The added experiential 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.

The contribution of social context to skill development and decision making is likely to vary as a function of the social relationships of participants in the setting (Cousi-Korbel and Frigaszy, 1995). This aspect of theory in social learning is addressed by several contributions in this volume. For example, van Schaik (Ch. 11; see also van Schaik *et al.*, 1999) discusses how social tolerance contributes to the appearance of technological traditions in apes. Perry *et al.* (Ch. 14) present exciting new data on the relation between extent of proximity and likelihood of sharing specific social interactional patterns and foraging behaviors in capuchin monkeys. Mann and Sargeant (Ch. 9) present information on similarities in foraging methods in mother and offspring dyads in dolphins. The significance of social tolerance to effective social learning is a central theme of many contributions in our volume.

It cannot be stated too often that social learning is not distinguished as a different kind of learning process than other learning. As far as we now know, there is no distinctive learning mechanism associated with social learning; there is no separate neural tissue devoted to social learning and there is no evidence for a "social learning module", as has sometimes been proposed by those adopting a modular perspective on cognition (e.g., Cosmides and Tooby, 1992). Nor is there any competition, so to speak, within the individual between reliance on social learning and reliance on individual learning. Sometimes quantitative modelers make an assumption that socially biased learning is distinctive in function or process from individual learning, but this is merely a convenient assumption used to explore the evolutionary consequences of different organizations of learning (e.g., Richerson and Boyd, 2000; Laland, Richerson, and Boyd, 1996). Our categorization of "social learning" as distinctive from "asocial learning" arises from the contextual elements only. A more

accurate characterization of these processes is the term socially biased learning (Frigaszy and Visalberghi, 2001).

The reader might at this point wonder about the issue of imitation, wherein an individual reproduces sequences of actions after observing another perform these sequences. Understanding how attention to observed action is coupled with the production of matching actions (as occurs during imitation), whether the actions are novel or familiar, is an important goal for cognitive scientists and neuroscientists (e.g., Byrne, 1999; Heyes and Ray, 2000; Myowa-Yamakoshi and Matsuzawa, 1999; Rizzolatti *et al.*, 1999; Whiten, 1998, 2000). Understanding the developmental trajectories, functional outcomes, and evolutionary pathways leading to imitation are also of value, particularly because imitation is a rare phenomenon. However, we can dismiss the notion that imitation is the *sine qua non* for traditions (shared behavioral patterns maintained in part by socially supported learning). A complete understanding of imitation will not lead to understanding how socially maintained practices arise in humans or any other taxon (Heyes, 1993; Heyes and Ray, 2000; Ingold, 1998). "Copying" behavior of others (as in imitation) is not a sufficient basis to produce skill; rather, skill requires repeated individual practice (Bernstein, 1996). Traditional practices are generated by each individual; they cannot be handed down as "units" from one individual to another, any more than the corporal bodies that perform them can be handed down (Ingold, 1998). Understanding how traditional knowledge and practice can be maintained requires a dynamic conception of the individual as engaged with its world, both social and asocial elements, in ongoing commerce.

In short, to understand the genesis of traditions we should strive to understand the nature of social bias in learning (where learning is broadly construed to include skill development). Nevertheless, in accord with the literature in this field, we use the term social learning to refer to the process in which social context contributes to skill development and decision making. When we understand how the social aspect of experience enables individuals to generate skills and adopt practices similar to those of their social partners, we may decide that some other label captures the process better. Until then, let us retain the categorical concept of social learning for comparative analyses of this phenomenon, realizing that it represents a construct about the context of learning, and not about the mechanisms of learning or distinctive neural structure. To conduct comparative analyses of social learning, we need to identify behaviors across

species that share a common benefit from exposure to, or interaction with, social partners for their generation.

1.5 Definition of tradition, and a model of “tradition space”

We focus on traditions in this work because they are an obvious link between social learning and evolutionary processes. A tradition is a behavioral practice that is relatively enduring (i.e., is performed repeatedly over a period of time), that is shared among two or more members of a group, and that depends in part on socially aided learning for its generation in new practitioners. Prototypically, a tradition is shared among most or all members of a group, although it could be maintained by just one dyad or just one class of individuals (e.g., members of one matriline, only juvenile females, etc.). A particular behavior cannot be identified as a tradition without inferring that socially aided learning supports its shared presence across individuals. 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 (Bikhchandani, Hirshlifer, and Welch, 1998; Boesch and Tomasello, 1998; Laland *et al.*, 2000); others restrict the term to behaviors that persist across generations (Heyes, 1993; McGrew, 1998; Sugiyama, 1993; Whiten *et al.*, 1999). In short, the temporal dimension of persistence of a shared practice can range from brief to the remainder of an individual’s life and beyond (in other practitioners); the shared behavior can be evident in as few as two individuals or extend 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. For our purposes, a measurable social contribution to the generation of the practice in new practitioners is necessary for a behavior to qualify as a tradition.

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 1.1 under the heading of the group process model, to emphasize that traditions are identified according to properties of

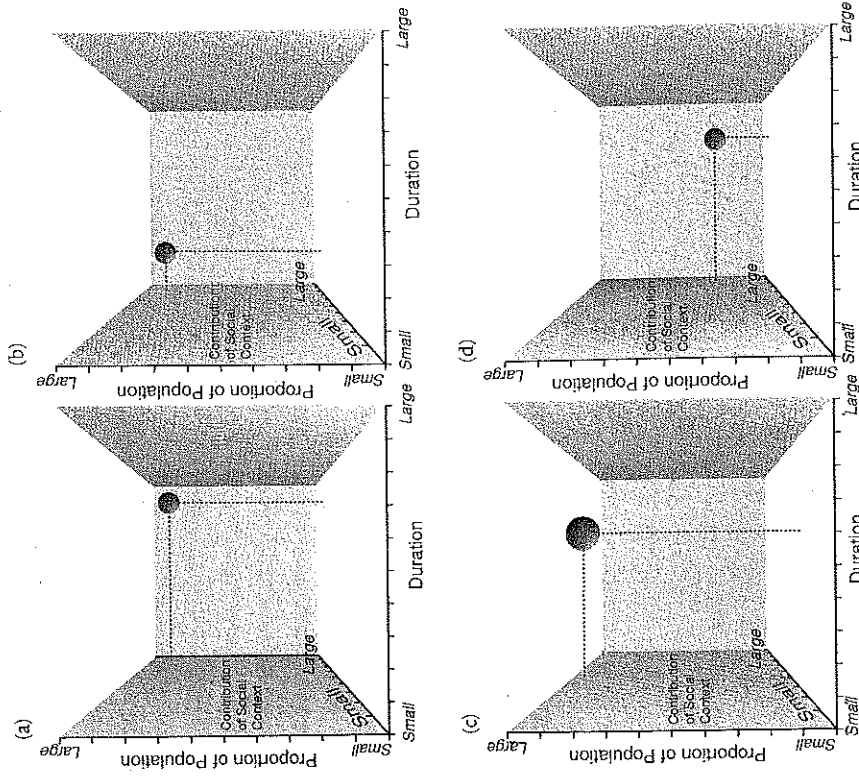


Fig. 1.1. The process model of traditions, conceived as a three-dimensional space. The defining axes are the duration of the behavior within the group (x axis), the proportion of the population displaying the behavior at any one time (y axis), and the contribution of social context to the acquisition of the behavior by new practitioners (z axis). Any distinctive behavior can, in principle, be placed into a unique location in this space. (a) A prototypical tradition: a behavior that is long-enduring, evident in most members of the group, and largely dependent on social context for its acquisition. (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).

behavior observed within a group. We use the term model here to mean a conceptual representation. 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

underlies, for example, the listing of behavioral variations in chimpanzees studied at different field sites published by a consortium of field observers (Whiten *et al.*, 1999), or the compendium of behavioral variations seen in cetaceans published by Rendell and Whitehead (2001). It is evident in several of the chapters in this volume as well, as a starting point to identify candidate traditions (e.g., Chs. 11 and 14). McGrew (1998) 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, as exemplified most elegantly in the work of Terkel and Aisner with rats (Terkel, 1996; see Ch. 6).

While the group contrast model may be a useful starting place to identify candidate traditions, it cannot be the ending point. 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 the question, "Is behavior X traditional in population Y?" 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 set the stage by indicating some behaviors that are likely to be acquired in part through social learning. As Dewar (Ch. 5) points out, 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. Huffman and Hirata (Ch. 10) discuss this issue in relation to the phenomenon of stone rubbing observed in many free-living groups of Japanese macaques.

The standard model of identifying traditions is illustrated in Fig. 1.2 under the heading group comparison model as a three-dimensional space, where the axes are degree of phylogenetic relatedness (genetic similarity), degree of behavioral similarity, and degree of environmental/ecological similarity. Here, the similarity between two or more groups is measured at one point in time. 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), they inhabit similar microhabitats, but they vary distinctly in the form of behavior X. Often the behavior pattern is widely evident in each population, 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, we reiterate, can suggest candidate traditions but it does not get at the essence of what a tradition is: a behavior pattern shared among members of a group that

influences for their generation in new practitioners occupy one quadrant of this space (as in Fig. 1.1a). Behaviors meeting these criteria fall clearly within the common meaning of the term tradition. How far down or out from this quadrant can we go in tradition space and still identify a behavioral practice as a tradition? To give three examples, what about behaviors that are relatively ephemeral but widespread and highly dependent on social influences (depicted in Fig. 1.1b)? Or behaviors that are long lasting and widespread within a group but are not strongly dependent on social influences (in other words, that are often independently generated; as depicted in Fig. 1.1c)? Or behaviors that are clearly dependent on social influences for their generation but appear only in a few individuals within a group (depicted in Fig. 1.1d)? Of these last three examples, can we call all three traditions? Do we need to subdivide this concept to do justice to these three dimensions? Different contributors to this volume express different points of view on this related set of problems. The debate is useful for our efforts to develop theoretical models of traditions as biologically important phenomena.

This perspective on traditions is at variance with the usual way comparative biologists 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, (a) the degree of similarity of the behaviors seen in different social groups, (b) the (usually hypothetical) degree of genetic and behavioral exchange among members of different groups, and (c) the extent of environmental similarity across sites inhabited by different groups. We shall refer to this paradigm as the group contrast model of traditions, also called regional contrast by Dewar (Ch. 5) and method of elimination by van Schaik (Ch. 11). The argument goes like this.

1. Group X and group Y are currently or until very recently members of a single breeding population (i.e., 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.

This model relies on characteristics unrelated to an essential feature of traditions: their dependence on social context for acquisition by new practitioners of the practice in question. However, this is the model that

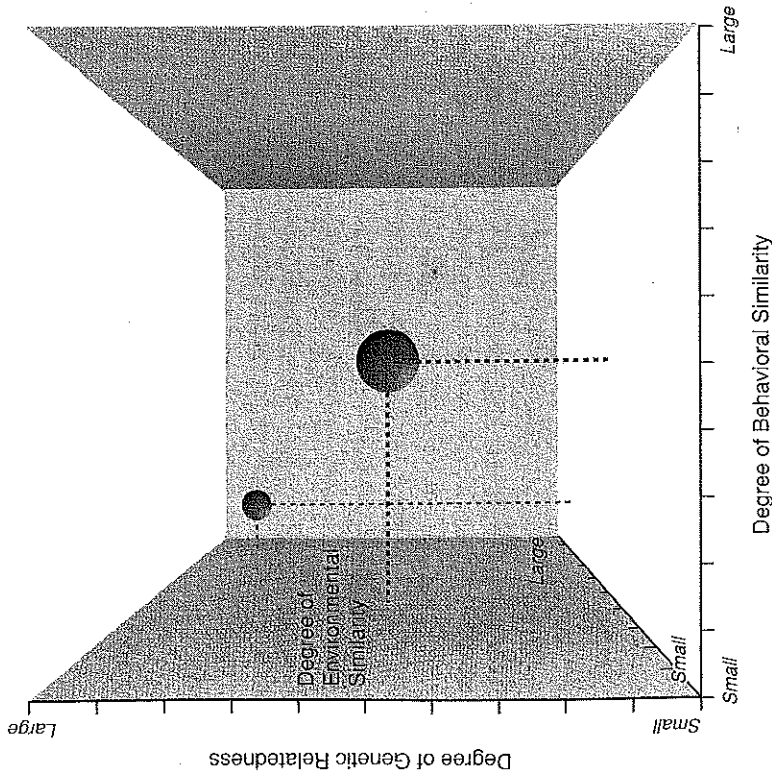


Fig. 1.2. The group comparison or regional contrast model of tradition conceived as a three-dimensional space. The location in space here defines the relation between two or more groups: the degree of similarity for the behavior of interest (x axis), the degree of genetic similarity for the groups under 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 showing 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.

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: behavioral differences between groups. Unfortunately, other processes besides social learning can lead to the same outcome, and this model cannot discriminate false positives (behavioral differences that are dependent on asocial factors and independent of socially aided learning). 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 Fig. 1.2 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 pattern 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.

All too often this model has been accepted as the best method available for identifying traditions in nonhuman animals. We argue instead that the group comparison model is logically inadequate to allow strong conclusions about the status of any behavior as a tradition. To accept that a behavior is a tradition with this model one must confirm two null hypotheses: no genetic differences and no environmental differences (sufficient to account for the observed difference). These can never be "proven" to the skeptics' satisfaction. On top of that problem of logic, the notion that explanations of differences at the genetic or environmental level can support or rule out explanations at the ontogenetic level is clearly mistaken. This notion was thoroughly discredited years ago by the compelling arguments of Lehman (1970) and others, who argued for an epigenetic understanding of individual development. Ontogenetic phenomena require an explanation in terms of individual ontogeny, not static notions of environmental conditions or genetic endowments. Social learning occurs during an individual's life; traditions are an outcome of several individuals' development. Social learning phenomena must (ultimately) be explained in terms of their development.

Why do behavioral scientists still feel compelled to exclude a genetic explanation for a behavioral character before they can consider how a behavior is acquired? Probably because they are confused as to what level of explanation a "genetic difference" affords. As Lehman (1970) points out, the terms innate, inherited; and their relatives (e.g., hereditary, heritable) have two quite different meanings that are often confused. One meaning, used by geneticists, is that a character is inherited if variations of this character across individuals can be shown to arise from differences in the genetic constitution of the different individuals. The term

is reserved for observed variability of the character in individuals with different genomes observed in the same environment; it implies "achievable by natural selection or by artificial selection". It does *not* address the question of whether variations in the environment during development would have an effect on the adult phenotype. The same genome can be associated with entirely different phenotypes in differing environments, and an environmental difference that greatly influences phenotypic development of one genome may have no effect on another, as demonstrated by Haldane more than half a century ago (Haldane, 1946). A straightforward example of the first principle is the variation across individuals and populations in parthenogenetic species, for example in whiptail lizards as documented by Taylor, Walker and Cordes (1997).

The second meaning often attributed to the terms innate, hereditary, or inherited is that of developmental fixity, the notion that a behavioral character is so developmentally canalized that it appears reliably even in the face of highly variable individual circumstances. This is an entirely different concept to the one discussed above; it has no bearing on "achievable by natural selection". It also has no bearing on what processes play a role in the behavior's development. Not keeping the two meanings distinct can lead to confusion. For example, to use the observation that the behavior of hybrid offspring matches that of both of its parents (in accord with first meaning accorded by geneticists) as evidence that a behavior is "innate" and, in the same sentence, that learning does not appear to influence the development of the behavior (in accord with the second meaning) reveals confusion about what innate means. (See Gortlieb (1992) for further discussion of how these concepts have been confused in the history of genetics and psychology.) Further, the pernicious and false notion that every element of behavior ought, on logical grounds, to be classifiable as "innate" or "learned" obscures serious consideration of how behaviors of interest develop. As Lehman (1970, p. 33) said, "The distinction between 'innate' and 'acquired' is an inadequate set of concepts for analyzing development."

We believe that the logical inadequacies of the group comparison model (or as Dewar, (Ch. 5) labels it, the regional contrast 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. The model implies that a "genetic differences" explanation can supercede an "acquired" explanation as the source of

a behavioral difference between groups. In actuality, these explanations are independent of one another. The model also requires the logically impossible procedure of confirming null hypotheses. As the model is logically inadequate, alternative interpretations can never be excluded, and the claim for tradition is necessarily weak. But is this unsatisfactory state of affairs necessary? We 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. In the next section and in our concluding chapter, we consider what kinds of evidence we should be collecting that can bear more deeply on the question of whether traditions exist in nonhuman species.

1.6 The comparative method in ethology

As MacLarnon (1999) reminds us, John Mill (1872/1967) explicated the principles of logical induction that govern the scientific enterprise today. Mill laid out four methods of inductive reasoning using comparative evidence: agreement, disagreement, residues, and concomitant variation. The first two methods rest on the principles that we can conclude that a causal relationship, or an enabling relationship, exists between a certain condition and the phenomenon under study by comparing (a) two instances in which a phenomenon occurs and the comparison groups have only one element in *common* (agreement) or (b) two instances in which a phenomenon occurs in one group but does not occur in another, where only one element is *different* between the comparison groups (disagreement). 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.

Phenomena in the natural world, where experimental manipulations are less frequently possible, rarely lend themselves to the strict standards of evidence required by the methods of agreement or disagreement, or their union (joint agreement and disagreement). In the natural world,

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 logic of this method parallels that of the recently developed CAIC method (comparative analysis by independent contrasts: Harvey and Purvis, 1991; Purvis and Rambaut, 1995) used in phylogenetic contrasts, which takes into account the degree of relatedness of the various taxonomic groups used in the analysis (see Ch. 3).

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 is always present but 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 (Ch. 11) 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 Ch. 14. In this case, the pair is the unit of analysis.

Neither of these methods provides the clear evidence of causal or conditional relationship that the first two methods do. Rather, they allow us to make the best use of available information; they provide correlational evidence concerning categorical or scalar variations of relevant variables across conditions. 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.

The comparisons envisioned by Mill to identify the contributions of some condition to the occurrence of a phenomenon are widely used in ethology and other sciences. They do not exhaust analytical strategies, however. We have an arsenal of other methods that support analysis of development. Developmental analyses are concerned with *how* a characteristic comes about: how something changes through time in an individual. In the case of behavior, longitudinal observations of an individual, or a set of individuals, provide the most powerful analyses. Data of this sort relevant to understanding the origins of traditions in nonhuman animals come from studies of vocal learning in many taxa, but especially in birds (see Ch. 8). The now-classic developmental studies of Terkel (Terkel, 1996) demonstrating the development of pine-cone stripping in young black rats whose mothers use this method of feeding have already been mentioned above. Mann and Sargeant (Ch. 9) provide data of this type for bottlenose dolphins. In nonhuman primates, the best examples of developmental studies relevant to understanding the origins of shared practices are those of stone handling in Japanese macaques (Ch. 10), the development of nut cracking in young chimpanzees (Inoue-Nakamura and Matsuzawa, 1997), and the development of various feeding techniques in young orangutans (Russon, 2003 and Ch. 12).

1.7 Standards of evidence: experimental and observational

What evidence do we require to determine that social learning has occurred? In the laboratory, social learning can be documented by its outcome in accord with the methods of agreement, disagreement, or joint agreement and disagreement. In a common design, we compare two groups of subjects. In the first group (the "social learning group"), individuals differ measurably at the outset in the manner of achieving something (e.g., finding food). Subsequently two or more individuals jointly behave in the same environment, either simultaneously or sequentially. In the second group (the "individual learning group"), individuals do not behave jointly in the same environment; they encounter the same circumstances on their own. Thus the individuals' exposure to the circumstances is the same across groups, but the social context of their experience is different. We conclude that social learning has occurred if members of the social learning group alter their behavior to be more similar to their social partner's behavior following joint exposure, compared with subjects that encounter the same problems individually. Usually in this design, one or

more individual(s) in the social learning group is more proficient at the task (and serves as a "demonstrator" to the others). The hypothesis to be tested is that the less-proficient individuals in the social learning group will become more proficient following exposure to the demonstrators than will members of the individual learning group following equivalent exposure to the problem, but without a demonstrator. In other words, exposure to the situation with a demonstrator allows the learner to behave more like the demonstrator more quickly than a solo learner alters its behavior to be more proficient (and more like the social group's demonstrator). Galef's studies of social learning of food preferences in rats (Ch. 6) and Visalberghi and Addessi's studies of food choices in capuchin monkeys (Ch. 7) illustrate the subtleties of experimental design that can follow from this logic.

A second common experimental design in social learning experiments is the "two action design", in which two or more groups of subjects encounter the same problem with a demonstrator-partner. The solutions practiced by the proficient partner vary in key ways between the groups; for example, in one group the demonstrator may pull up a lid to open a container, and in another group the demonstrator may push the lid down to open the container. In this design, one seeks differential shifts towards the more expert partner's behavior on the part of the less-proficient partner in all groups, and the form of change is predicted to vary between the groups. Zentall (1996, p. 232) provides several examples of studies using this design (see also Fritz and Kotrschal, 1999; Voelkl and Huber, 2000).

Regardless of design or circumstance, as an individual acts in the environment, the consequences of its actions will impact whether or how often the behavior is performed again. Socially learned behaviors produce a history of consequences, as do all behaviors (Galef, 1992). In this sense, the methods of agreement and disagreement are not a perfect fit to the problem of demonstrating social learning, as behavior has a historical component that these logical principles do not encompass. For example, over time, a behavior may become modified or may become performed more selectively as a consequence of continuing practice, or it may be abandoned by some individuals. Unfortunately for the scientist interested in assessing the likelihood that a behavior is a tradition, all these processes have the net effect of masking the differences in behavior between groups that experienced different learning contexts at an earlier time. Comparisons of groups according to the consequences of experience at a single, earlier period may thus become muddled, especially as the temporal distance

between the different learning context and the evaluation of performance increases.

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 control group. Changes in performance may also reflect some concurrently varying feature of the situation (such as seasonal changes in the availability of resources, physical changes in the individual, and so on). This could be ruled out with a control group in the same context but shielded from social influence, but this is not possible in natural circumstances. Moreover, unlike in experimental studies, it is usually impossible to know any individual's level of experience with a task prior to the start of observations. Nevertheless, field observers can document social contexts in which behaviors occur and changes over time in individual performance; they can document intragroup variation in behavior at a particular time, and they can seek comparable evidence about specific practices in other groups of the same species or of related species. The contributions by field researchers in this book illustrate the application of these forms of logic to the analysis of behavior of many species of animal in natural settings.

Identification of locale-specific behaviors is not sufficient to conclude that social learning is a necessary element in the generation of those behaviors. Multiple pathways lead to similar behaviors in many instances. For example, Galef (1980) examined how rats could develop the habit of swimming under water to collect shellfish from the riverbank. This unusual manner of foraging is (or was) common in rats living at a certain location along the River Po in Italy (Gandolfi and Parisi, 1973). Diving for food seemed a strong candidate for a behavior fully dependent upon social learning for its persistence in the population. Nevertheless, Galef (1980; see also Ch. 6) showed experimentally that juvenile rats could acquire this habit readily without any social scaffolding in conditions similar in relevant ways to their riverbank habitat. Social learning might aid individuals to develop the behavior but the behavior is not necessarily dependent on social learning for its generation. We still do not know the extent to

which social learning does in fact contribute to the continuance of this practice in rats along the River Po (the residual in the method of residues), or indeed whether it contributes at all. It seems plausible, but it is not necessary.

Sometimes those conducting naturalistic observations argue that demonstrating the necessity of social learning in the generation of similar behaviors in different individuals requires excluding all plausible alternative explanations (usually, environmental sources, such as resource availability, and presumed genetic differences) (Boesch, 1996; McGrew, 1998). Unfortunately, it is a logical impossibility to exclude 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 also Ch. 5). 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 (a) how rapidly new practitioners develop the behavior with differing forms of social support, (b) how close the behavioral resemblance remains across links, and (c) 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.

Some authors emphasize the persistence of a behavioral pattern across biological generations as necessary to accord it the status of a tradition (e.g., McGrew, 1998; Whiten *et al.*, 1999). As may be surmised from the traditions space model provided in Fig. 1.1 and discussed earlier, we find this requirement too restrictive. Temporal stability is surely important for the evolutionary significance of a particular pattern. Traditions allow one generation to impact 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. Traditions can contribute to constructed niches (Laland *et al.*, 2000) and thus have effects on fitness. However, in theory, even ephemeral traditions (lasting only a portion of the individual's lifespan) can have fitness consequences. Vocal traditions in many taxa drift in less than a lifespan; degree of adherence to the traditional song of the moment can still influence individual fitness. As Pery *et al.* argue (see Ch. 14), other forms of social conventions may also have this consequence.

Documentation of socially aided learning by animals in natural settings is likely to remain challenging, whatever method is adopted for this purpose. Shifting social context and ongoing behavior of several individuals are not easy to record in real time. Even documenting intergroup variation in the presence or absence of a specific behavior can be difficult, because of the difficulty in interpreting negative evidence. Although statistical methods can be used to examine the probability of noting a behavior in one population given its rate of occurrence in another population, to evaluate whether the two populations produce the behavior at equivalent rates (e.g., see Ch. 11), interpreting behaviors seen at extremely low frequencies remains problematic.

However, the situation is far from hopeless. As contributors to this volume show, there are many different forms of evidence that can be brought to bear on the question of the third dimension in traditions, that of social contributions to the generation of the behavior in new practitioners. We anticipate that the sample efforts presented in this volume will generate new ideas for those studying many different taxa and forms of behavior about how to evaluate the contribution of social influences in their own cases of interest.

1.8 Conclusions

Our principal aim is to understand traditions as biological phenomena in order to improve our understanding of their contribution to the evolution and current life ways of various taxa. We have adopted an ethological stance to this problem, noting that we should recognize explanations at different levels (evolution, function, mechanism, and development) as having complementary value, and that explanations at these different levels should be compatible with one another. Ideally, we would like to create a model that effectively predicts when and in what domains

traditions will appear in a particular species, and how social influences will support the generation of shared behaviors, taking into account the species' constellation of ecological, social, and behavioral characteristics. We would like to model evolutionary trends in the occurrence of traditions, as well as ontogenetic patterns governing the acquisition of shared behaviors. We are far from reaching all these goals at present. Nevertheless, we are encouraged by the energy and creativity of the research community around this issue as represented by the contributions to this volume.

One of our central concerns in this chapter has been to lay out a definition for traditions that permits empirical rigor. To this end, we have suggested conceptualizing 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; see Fig. 1.1). This heuristic model makes it clear why documenting group specificity and long (even intergenerational) duration, 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 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.

Behavioral scientists work in settings ranging from the laboratory (where virtually every aspect of social context, individual history, and environmental circumstance can be monitored and controlled) to field conditions, where the observer must make do with incomplete information. Therefore, we must be prepared to make the best use of very different kinds of information. We must acknowledge the different forms of comparison enabled by the different circumstances we face in these different conditions of scientific inquiry, and we must adapt our analytical goals to the data supported by each condition. For those who study social learning, this means adopting the method of residues or the method of concomitant variation, to use Mill's terminology, to examine the critical dimension

of social contribution to shared practice when we cannot manipulate the relevant variables of social context and solo practice. Those who have the luxury (and the burden) of designed experiments can adopt the methods of agreement and disagreement (that is, traditional experimental methods). All of us have the responsibility to adopt longitudinal methods where possible, as developmental analyses are necessary to understand how shared practices arise.

Understanding traditions as biological phenomena requires the collaborative efforts of scientists working from diverse theoretical and methodological realms (modeling, experiments, and observations of behavior in natural settings). Although field observations will virtually never support the use of the stronger methods of agreement and disagreement, they can be a very rich source of information supporting other methods. In particular, two forms of information from naturalistic observations are relevant to studies of traditions: (a) behavioral variation within groups, in conjunction with patterns of social affiliations or (a less powerful method) across sites, and (b) longitudinal data on 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.

This chapter is followed by contributions by Laland and Kendall, Reader, Lefebvre and Bouchard, and Dewar (Chs. 2–5) addressing evolutionary, comparative, and process models of traditions. Chapters 6–14 cover a variety of taxa and of empirical approaches to the study of traditions. Several contributions illustrate the logic and power of analyzing naturally occurring patterns of variation with moderately longitudinal data (Chs. 9–12, 14). In Ch. 13, Boinski *et al.* describe the starting point for studies of traditions, a behavioral phenomenon that seems likely in their estimation to rely on social context for some aspects of its development. Contributions from experimental scientists (Ch. 6 by Galef, and Ch. 7 by Visalberghi and Addressi) illustrate how complementary use of the different comparative methods aids a full understanding of complex biological phenomena, and both provide cautionary examples of behaviors that seem likely to be dependent on social learning but that can arise rather easily in other ways. Janik and Slater (Ch. 8) review traditional aspects of vocal communication in birds and mammals to round out the topical and taxonomic coverage. In the final chapter, we draw out shared themes evident in these contributions to suggest directions for future work, and to highlight opportunities for fruitful collaboration.

At the end of the day, we must recognize that social learning, leading to traditions, is a central participatory feature in behavioral biology; it deserves our concentrated attention even though it is no more amenable to easy comprehension than any other aspect of behavioral biology. Developing clear conceptual and methodological approaches is a necessary first step in creating a rigorous field of study devoted to this subject. We intend that this book will stimulate progress in this endeavour.

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