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## Towards a biology of traditions

### 1.1 Introduction

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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

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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

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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

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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 Visalberghi, 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 of 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 a set of specific learning abilities. Big brains afford more modulated learning.

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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.

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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,



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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.



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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 asocial 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 (Fragaszy 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

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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, Fragaszy, 2000; Fragaszy 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 (Coussi-Korbel and Fragaszy, 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