

INTRODUCTION

Social learning research outside the laboratory: How and why?

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Social learning enables both human and nonhuman animals to acquire information relevant to many biologically important activities: foraging (Galef & Giraldeau, 2001; Mesoudi & O'Brien, 2008), mate choice (Jones, DeBruine, Little, Burriss, & Feinberg, 2007; Laland, 1994; White, 2004), conflict (Peake & McGregor, 2004), and predator avoidance (Griffin, 2004). Although use of social information is not *inherently* adaptive (Boyd & Richerson, 1985; Laland, 2004), its frequent roles in the development in animals of both innovations (sensu Reader & Laland, 2003) and routine skills (Jaeggi et al., 2010; Krakauer, 2005), as well as its exceptional prevalence in human societies, suggest the importance of social information in biological and cultural evolution. In fact, socially learned information may have been instrumental in promoting the biological evolution of cognitive capacities (Whiten & van Schaik, 2007), and variation in use of social learning as an inheritance system may be responsible for the disparity between human and nonhuman animals in the complexity of their cultural behavior (Tomasello, 1999; Whiten & van Schaik, 2007).

This special issue of *Learning & Behavior* has two inextricably linked foci: first, identification of social learning in natural contexts, and second, consideration of the implications of current findings from the study of social learning in natural contexts for understanding the evolution of cultural capacities in the animal kingdom, of which humans are an integral part. Although there are well-established, sophisticated methods for documenting social learning in the laboratory (see the issue of *Philosophical Transactions B* edited by Smith, Kalish, Griffiths, & Lewandowsky, 2008), laboratory studies often have limited ecological validity and are frequently not practicable, especially with large or endangered species (Figure 1). Most

importantly, without an understanding of social learning in the context in which it evolved, we cannot hope to elucidate the interaction between biological and cultural evolution. Thus, identification of social learning in free-living populations of animals is a necessary first step in our quest for knowledge. Unfortunately, until recently, researchers have been forced to rely on expert opinion when deciding what proportion of the behavioral variation observed in natural contexts can plausibly be accounted for by cultural, as opposed to ecological and genetic, processes. The result has been heated debate, which some have gone so far as to describe as “war” (McGrew, 2002), about the reality of purported cultural behaviors in animals.

The disagreement over the utility of describing local specific behaviors as cultural is a result of the inability of the approaches previously available to researchers who study free-living populations (e.g., the *group-contrasts method* or *method of exclusion* pioneered by Whiten et al., 1999; quantitative analyses pioneered by Sargeant & Mann, 2009; Whitehead, 2009) to conclusively determine whether social learning is required in order to produce the observed patterns of behavioral variation. Despite the increasing number of high-profile, and oft-debated, reports of “culture” in wild animals (Hohmann & Fruth, 2003; Leca, Gunst, & Huffman, 2007; Perry et al., 2003; Rendell & Whitehead, 2001; van Schaik, Ancrenaz, et al., 2003; Whiten et al., 1999), until we have tools that can provide widely accepted evidence for social learning, controversy and confusion will reign both as to the extent of culture in animals and the utility of studies of animal traditions in understanding animal and human evolution (Galef, 2009).

Over the last decade, and especially in the last few years, a variety of methods have emerged for identifying (the consequences of) social learning in natural contexts

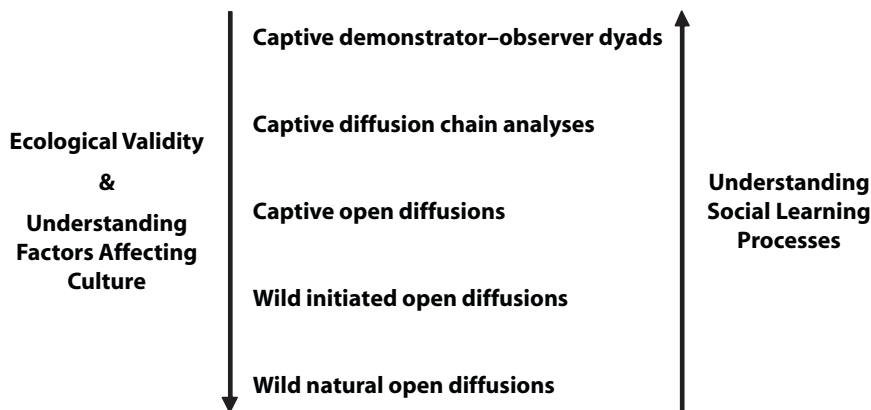


Figure 1. An illustration of how methods for identifying social learning lie on a continuum. At the top of the list, there is good control and understanding of social learning processes and relatively little ecological validity, whereas toward the bottom there is increased ecological validity but decreasing likelihood of even distinguishing social from asocial learning. The term *wild initiated open diffusions* refers to cases in which the experimenter provides a novel task, thus initiating the inception and spread of information. For further discussion of social diffusion experiments, see Whiten and Mesoudi (2008) and Mesoudi and Whiten (2008).

(i.e., in social groups, whether in the wild or captivity and whether involving one or multiple groups). These methods are summarized in Table 1, which, although it is not exhaustive, may be used as a guide to the ever-growing toolbox available for the capture of social learning in natural contexts. It is timely to bring such methods together to highlight and assess this growing toolkit, available to researchers interested in both animal and human culture. These methods will be a focus throughout this special issue, and include (1) intensive field observation, allowing culture to be inferred as a consequence of eliminating any substantial role for ecology, genetics, and developmental constraints in producing observed variation (in this issue, see Holzhaider, Hunt, & Gray, 2010; Lonsdorf & Bonnie, 2010); (2) theoretical/statistical methods for assessing the likelihood of asocial learning being responsible for an observed pattern of behavior, which permit inference of social learning when asocial learning has been deemed improbable (Franz & Nunn, 2010; Hoppitt, Kandler, Kendal, & Laland, 2010; R. L. Kendal et al., 2010); (3) fitting mathematical models to phylogenetic data (Lycett, 2010); and (4) use of novel field (Reader & Biro, 2010; Thornton & Raihani, 2010) and naturalistic (Caldwell & Millen, 2010; Flynn & Whiten, 2010) experiments. These new methods, and the associated findings, involve not only a wide array of species (including fish, birds, mammals, nonhuman primates, and both child and adult humans), but also a wide array of factors that may have affected both biological and cultural evolution (including different social learning processes, ecology, social systems, developmental constraints, and individual differences).

This special issue is the first both to focus on the new and exciting methods now available to the social learning researcher (summarized in Table 1) and to emphasize the potential and utility of ecologically valid studies of cultural transmission. Although we still face a challenge in ascertaining which social learning processes underpin the transmission of behavior patterns in free-living ani-

mals (see Hill, 2010, in this issue; but see J. R. Kendal, Kendal, & Laland, 2007; Thornton, Samson, Laland, & Hoppitt, 2010), we have come far, at least in our ability to identify social learning in natural contexts. Note, however, that despite any methodological shortcomings, previous field studies have shown what minimally constitutes animal cultures or traditions, allowing us to infer the most likely foundation from which human culture has arisen. The proliferation of methods for capturing social learning in natural contexts that is highlighted here would not have occurred without these earlier field studies, and indeed many of the new methods may be applied fruitfully to existing data sets. For example, the option-bias analysis method (R. L. Kendal et al., 2010) is in essence a quantitative version, using individual-level information, of the widely used ethnographic or group-contrasts method (van Schaik, Ancrenaz, et al., 2003; Whiten et al., 1999).

We hope the reader will agree that the field of social learning has reached a point at which the efforts of researchers from diverse backgrounds, producing a coalescence of statistical tools, field and laboratory approaches, and insights regarding a variety of species, are enabling the study of the evolution of culture in ways unimagined when, over half a century ago, the social transmission of naturally occurring and experimentally seeded innovations was first described in wild populations (Fisher & Hinde, 1949; Kawai, 1965). Furthermore, as a result of the creation of methodologies allowing valid comparisons of humans and nonhumans, the present collection of articles may help bridge the divide between biological anthropologists, who often deem social learning sufficient for defining traditions or culture, and social/cultural anthropologists, who most often assert that social learning is necessary, but not sufficient, for the emergence of culture (Hill, 2010).

The findings of the research highlighted here enter into the present debate regarding the extent of culture in animals and the processes by which the potent cultural capacity of humans has evolved. The field of animal social learning

Table 1
A Guide to Methods for Capturing Social Learning in Natural Contexts in Human and Nonhuman Animals

Method	Appropriate Data Types			Group Numbers		Behavioral Traits		Other Data Required
	Snapshot	Diffusion	Developmental	One	Multiple	One	Multiple	
Field observations (Huffman, Nahallage, & Leca, 2008; Lonsdorf & Bonnie, 2010)	✓	✓	✓	✓	✓	✓	✓	Social dynamics, dispersal, local ecology, demographic factors, etc.
Group-contracts method/method of exclusion or elimination (pioneered by Whiten et al., 1999)	Variation in behavior not attributed to ecology or genetics			Krützen et al. (2005); van Schaik, Fox, & Fechtman (2003)	van Schaik, Ancenaz, et al. (2003); Whiten et al. (1999)	✓	✓	Detailed local ecology and genetic relatedness between individuals/groups
Multivariate/multifactorial analytical methods (Sargeant & Mann, 2009; Whitehead, 2009)	Similarity between individuals in a behavioral trait		Similarity between individuals in a behavioral trait	✓	✓	✓	✓	Matrices of similarity between individuals in ecology, genetics, and association patterns
Cue reliability approach (Dewar, 2003) (This method has been proposed but not yet used outside the laboratory.)	Is social learning needed in attempting an <i>adaptive but potentially dangerous</i> behavior?			✓	✓	✓	✓	Estimation of individual "reliability thresholds," nonsocial and social cue "reliability"
Diffusion curve analysis (Franz & Nunn, 2009; Hoppitt, Kandler, et al., 2010; Reader, 2004)		Use <i>not</i> recommended by cited authors!		✓	✓	✓	✓	Social dynamics of group
Analysis of the spatial spread of a trait (Lefebvre, 1995)		Also "wave of advance" (Ammerman & Cavalli-Sforza, 1984)		✓	✓	✓	✓	Spatial and temporal distance of each new trait observed from the presumed innovation origin
Phylogenetic method (e.g., chimpanzees; Lycett, 2010; humans; Tehrani & Collard, 2002)	Prevalence of behavioral trait in each group			✓	✓	✓	✓	Genetic relatedness within and between groups; for humans, relevant social/political changes
Fitting mathematical models to observed human data (e.g., Cavalli-Sforza & Feldman, 1981; Hahn & Bentley, 2003)	✓	✓		✓	✓	✓	✓	Parameter values required for the specified model
Bass forecasting model predicting the spread of human innovations (see Rogers, 2003, p. 208)	Time of acquisition			✓	✓	✓	✓	Adoption due to (1) mass media, (2) interpersonal communication channels, and (3) index of market potential

Table 1 (Continued)

Method	Appropriate Data Types		Group Numbers		Behavioral Traits		Other Data Required
	Snapshot	Diffusion	Developmental	One	Multiple	One	
Identifying teaching (Thornton & Raihani, 2010)			Improvement in pupil performance	✓	✓	✓	Satisfy Caro & Hauser's (1992) criteria: teacher behavioral modification when naive present; cost (or lack of immediate benefit) to teacher; "learning" by pupils
Primate archeology (Haslam et al., 2009)	Emphasizes repeated use of sites for tool use or sleeping			✓	✓	✓	Studies of tool use in extant human and non-human primates
Methods Applicable to Observation of Preexisting and Experimentally Induced Behavior Patterns							
Network-based diffusion analysis (Franz & Nunn, 2009, 2010; Hoppitt, Boogert, & Laland, 2010; Hoppitt, Kandler, et al., 2010)		Time of acquisition and order of acquisition		✓	✓	✓	Social network (e.g., proximity/grooming/tolerance during foraging); individual variables (e.g., asocial learning); understanding of task structure effects
Pairwise similarity matrices and cluster analysis (Bastian, Zweifel, Vogel, Wich, & van Schaik, in press; Matthews, 2009; Perry et al., 2003)	Frequencies with which each trait used per individual			✓	✓	✓	Matrices of individuals in proximity during others' trait use
Predicting the spread of innovations using linear models (Boogert, Reader, Hoppitt, & Laland, 2008)		Time of acquisition and order of acquisition		✓	✓	✓	Group-dependent (e.g., association patterns/social rank) and group-independent (e.g., neophobia/asocial learning abilities) variables
Option-bias analysis (R. L. Kendal et al., 2010; R. L. Kendal, Hoppitt, & Laland, 2009)	Frequencies with which each option/trait used per individual			Monte Carlo method	χ^2 /LLM/GLM randomization methods	χ^2 /LLM randomization methods	Underlying bias(es) in option use; asocial learning rate; social dynamics (e.g., subgroups/cliques)
Modeling predictive function of observation for behavior (Perry, 2009)		Individuals' frequencies of <i>observing</i> each trait being used by a conspecific & of <i>using</i> each trait themselves		✓	✓	✓	Useful to know trait efficiencies, kin relations, social dynamics

Table 1 (Continued)

Method	Appropriate Data Types		Group Numbers		Behavioral Traits		Other Data Required
	Snapshot	Diffusion	Developmental	One	Multiple	One	
Modeling social learning processes (J. R. Kendal, Kendal, & Laland, 2007; Thornton, Samson, Laland, & Hoppitt, 2010)		Determine role of different learning processes		✓	✓	✓	Which individuals observed each task manipulation and their location; social dynamics within group
Comparing genetic, geographic, and cultural distances (e.g., Hewlett et al., 2002)	✓				✓	✓	Distance measures
Experimental Methods of Investigating Social Learning in Natural Contexts/Social Groups							
Field experiments (reviewed in Reader & Biro, 2010; e.g., Holzhaider et al., 2010; R. L. Kendal et al., 2010)		For example, use of demonstrators, translocations, or playback	Provisioning (Holzhaider et al., 2010; Thornton & McAuliffe, 2006)	✓	✓	✓	Social dynamics; demographic and ecological factors; etc.
Combined methodology of captive experiments and observations in the wild (e.g., Galef, 1980; Zann, 1990; for reviews, see Galef, 2004; Whiten, 2009)	✓	✓	✓	✓	✓	✓	Relation of laboratory findings to development of behavior in the wild (Galef, 1984)
Diffusion studies (reviewed by Flynn & Whiten, 2010 [children]; Whiten & Mesoudi, 2008 [animals]; Mesoudi & Whiten, 2008 [humans])		Various levels of experimentation to track trait matching of individuals during the diffusion of information		✓	✓	✓	Social dynamics between individuals (diffusion chains) and among group (open diffusions)
Investigating cumulative culture in humans (Caldwell & Millen, 2010)		Skill improvement at end of diffusion chain		✓	✓	✓	Interactions (e.g., teaching) within groups during diffusion chain
Virtual experiments of putative cultural transmission (e.g., Fay, Garrod, Roberts, & Swoboda, 2010; Gürek, Irlenbusch, & Rockenbach, 2006; Mesoudi & O'Brien, 2008; Salganik, Dodds, & Watts, 2006)		Individuals interact in a computer/Web "game"		✓	✓	✓	Observed data, computer simulations, and participant motivations
Model fitting of social learning strategies (e.g., Kameda & Nakamishi, 2003; McElreath et al., 2008; Rendell et al., 2010; Toelch et al., 2009)		Individuals or strategies interact in a computer "game"		✓	✓	✓	Evolutionary computer simulations, participant motivations

Note—This nonexhaustive table provides details regarding how various methods have been, and may be, used to capture social learning in natural contexts involving group(s) of freely interacting individuals (✓ = yes). For example, a given method may have been applied to a single data set consisting of one group/trait, but may have the potential to be applied to several. The term *snap/shot* implies that the researcher does not have to observe the inception and consequent diffusion of a novel behavior to use the method in question, and consequently may collect the data required to employ the method over days, weeks (e.g., frequency of behavior per individual), or years (e.g., the roles of ecology or genetics in the distribution of a behavior).

needs to provide an estimate of the importance of social learning and traditions in the development of the behavioral repertoires of natural populations, as well as (1) a theory predicting the conditions in which traditions do and do not occur (e.g., R. L. Kendal et al., 2010; Lonsdorf & Bonnie, 2010; Reader & Biro, 2010) and (2) a theoretical framework for understanding the evolution of different mechanisms of social learning (e.g., teaching [Thornton & Raihani, 2010] or collaboration [Flynn & Whiten, 2010]). These may be distant vistas, but this collection of articles highlights the tentative steps the field is making toward their realization.

It remains to be seen whether traditions in animals provide any insight into the evolution of human culture. On the one hand, knowledge of animal traditions does *not* inform the study of human culture, because the mechanisms that maintain human culture and animal traditions are probably not homologous (Galef, 2009). Thus, cognitively more advanced species possess a variety of social learning mechanisms used in the acquisition of skills and knowledge. Consequently, it is inevitable that humans and other animals use different sets of mechanisms when engaging in social learning (Subiaul, 2007). For example, it is becoming clear that teaching plays an infinitely greater role in the acquisition of behavior in humans than in our great ape relatives, although, interestingly, behaviors that meet the criteria explicit in the most frequently used definition of teaching (Caro & Hauser, 1992) are also found in some unexpected places (e.g., meerkats, pied babblers, bees, ants, cats; see Thornton & Raihani, 2010; for a review, see Hoppitt et al., 2008). Indeed, the emergence of novel social learning mechanisms in different lineages is to be expected, and describing and analyzing such emergent mechanisms is an important part of the exploration of species differences. Obviously, taxa lacking particular mechanisms of social learning are incomplete models for taxa that do possess them.

On the other hand, even if the *mechanisms* used to establish and maintain cultural phenomena are clearly not homologous, the *phenomena* of traditions or cultures themselves may well be homologous between humans and some nonhuman species. Indeed, exploration of differences in the mechanisms supporting traditions in different lineages will suggest selective contexts in which novel mechanisms could have arisen. An understanding of social learning in wild animals may therefore provide a general theory of cultural evolution highlighting which cultural features are present and absent in nonhuman species and the causes of the unique cultural capacity of humans (Hill, 2010). The cultural repertoires of humans are far larger than those of any nonhuman animal (Lycett, 2010), probably because of the presence of cumulative culture in humans (Caldwell & Millen, 2010) and its absence in other animals (but see Holzhaider et al., 2010). Still, exploration of differences between the mechanisms and breadth of human and animal cultures should inform scenarios of human evolution, just as differences between the traditions of monkeys and great apes, or of corvid and noncorvid birds, should inform scenarios of the evolution of culture in those lineages.

Knowledge of social learning in natural contexts also has implications for ethics, philosophy, and politics. Continuity of the human and the nonhuman animal mind affects ethical considerations in animal welfare. Similarly, an understanding of social learning in natural circumstances can be used to enhance the conservation and management of species facing extinction, as well as influencing conservation priorities through increasing awareness of the existence of not only genetic, but also cultural diversity in animals (see Whitehead, 2010, in this issue).

We hope that this collection of articles, along with those summarized in Table 1, provides at the least a first step toward general acceptance of a methodological toolbox for identifying social learning in natural contexts. Indeed, we are convinced that the only way to bring peace to the culture “wars” (McGrew, 2002) is to stimulate further rigorous study of traditions (or culture) in naturalistic contexts.

AUTHOR NOTE

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