

CAPTURING SOCIAL LEARNING IN NATURAL CONTEXTS

Opportunities and constraints when studying social learning: Developmental approaches and social factors

ELIZABETH V. LONSDORF

*Lester E. Fisher Center for the Study and Conservation of Apes, Chicago, Illinois
and University of Chicago, Chicago, Illinois*

AND

KRISTIN E. BONNIE

*Beloit College, Beloit, Wisconsin
and Lester E. Fisher Center for the Study and Conservation of Apes, Chicago, Illinois*

Identifying social learning in wild populations is complicated by the relative lack of ability to conduct controlled experiments in natural habitats. Even in more controlled captive settings, tracking the innovation and spread of behavior among known individuals can be challenging, and these studies often suffer from a lack of ecological validity. In recent years, a host of new approaches have been undertaken to attempt to provide more quantitative control and empirical demonstration of social learning, both in the wild and in captive settings that more closely mimic natural contexts. Developmental approaches are being undertaken more regularly that allow us to study the ontogenetic trajectory of complex skills in a variety of taxa. Likewise, a spirited focus on the social context of social learning has emerged, and researchers have begun to meticulously analyze the influences of social systems and the characteristics of demonstrators and observers. Here, we provide a review of these studies and summarize the opportunities and constraints that exist when one attempts to study learning in social species. We suggest that although the study of social learning in nonhuman animals is becoming much more complex, addressing this complexity provides a fruitful model for understanding the evolution of human cultural behavior.

“Monkey see, monkey do” is a phrase commonly used to describe behavioral mimicry among young children. Data gathered from around the animal kingdom demonstrate that if individuals “see,” they very often “do.” However, recent research has increasingly shown that this “monkey see, monkey do” process, known as *social learning*, is not always straightforward and is commonly affected by the social dynamics that exist among individuals and the social setting in which they find themselves.

Anthropologists, psychologists, and behaviorists have long been intrigued by the task of untangling the transmission processes, developmental trajectories, and cognitive requirements of behaviors that are purported to be learned socially. But social learning is exceedingly difficult to study in wild animals, due to a combination of the lengthy observation times necessary to capture behaviors that may be rare, the long developmental period of some species

(in which many such behaviors are learned), and the lack of an ability to conduct the requisite experimental controls. As a result, few field studies provide strong evidence for social learning in wild populations (Laland & Janik, 2006), although more examples are beginning to emerge within the literature (see below). In the simplest of terms, in order to conclude that social learning has taken place, researchers must observe a novel behavior and be able to test that its presence is related to interaction with an experienced individual (or its products) and is not a result of ecological or genetic causes (West, King, & White, 2003). In field studies of wild animals, this is largely impossible, which has resulted in a variety of approaches taken to try to quantify social learning in other ways. Although statistical and mathematical modeling techniques are increasingly prevalent within the literature (see, e.g., Franz & Nunn, 2010; Hoppitt, Kandler, Kendal, & Laland, 2010; Kendal

E. V. Lonsdorf, elonsdorf@lpzoo.org

et al., 2010; Lycett, 2010), the two most predominant approaches remain ethnographic and experimental. The ethnographic method pools observational data from intensive and long-term field studies and infers social learning as the causative agent for differences between social groups when genetic or ecological explanations seem implausible (bonobos, Hohmann & Fruth, 2003; capuchin monkeys, Perry et al., 2003; cetaceans, Rendell & Whitehead, 2001; orangutans, van Schaik et al., 2003; chimpanzees, Whiten et al., 1999). This approach contributes valuable quantitative measures of scope of behavioral variation but still seeds much debate on controlling for genetics and ecology (Laland & Hoppitt, 2003; Laland & Janik, 2006; Lycett, Collard, & McGrew, 2007, 2010; McGrew, Ham, White, Tutin, & Fernandez, 1997). The aim of experimental methods with captive individuals (groups or, more often, pairs of individuals) is to control for and delineate the cognitive processes thought to support social learning (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Therein lies the conundrum, or *gap* (Whiten & Mesoudi, 2008); that is, in most reports of social learning among wild populations, social learning is inferred from existing behavior patterns, rather than studied over the developmental trajectory of behavior. The underlying learning processes are difficult to determine in the field, and the diffusion is tricky to track, since the initial innovation is rarely observed and the patterns of association between individuals are rarely well known. In contrast, studying social learning in experimental settings allows for control of behaviors and relationships between individuals, but then suffers from a lack of ecological validity and may not reflect transmission patterns in the wild. A happy medium may be *natural experiments*, where different wild animal groups are seeded with alternative behaviors and transmission is carefully documented (Kendal et al., 2010; Whiten & Mesoudi, 2008), or studying free-ranging populations in protected areas that, although provisioned regularly (e.g., the capuchin monkeys in Brazil; Ottoni & Izar, 2008), also show natural wildlike foraging and social behavior. We refer the reader to Reader and Biro (2010) for a detailed review of these studies.

Adding to the complexity of studying social learning is the breadth of behaviors that animals may acquire socially—from behaviors with important fitness consequences, such as foraging and predator detection, to “arbitrary” behaviors such as idiosyncratic gestures or vocalizations (e.g., stone handling in Japanese macaques, Huffman, 1996; raspberry vocalizations in orangutans, van Schaik et al., 2003; arbitrary conventions in chimpanzees, Bonnie, Horner, Whiten, & de Waal, 2007). The picture is further clouded by the increasing assortment of taxa, including fish, birds, and mammals, that are thought to show social learning and the diverse range of developmental and social systems that are represented in these species. Transmission of behaviors can occur vertically (from adult to offspring) or horizontally (between conspecifics outside of the parent–offspring relationship), and a myriad of proposed mechanisms have been defined, studied, and debated (see Hoppitt & Laland, 2008).

Since social learning is proposed to be a key driver of cultural differences among populations, an understanding of the dynamics and factors affecting social learning gives us insight into human and nonhuman cultural evolution. However, as we detail below, untangling and identifying these important factors is no small task, and approaches may necessarily vary depending on the study setting and species. Here, we provide a review of two main areas: developmental approaches to studying social learning that more closely mimic how learning occurs in the wild and methodological considerations of social factors that likely influence transmission in natural settings. We provide a broad, if not exhaustive, review of both field and captive studies in order to illustrate the methodological issues that warrant consideration when one attempts to document social learning in group-living animals.

DEVELOPMENTAL APPROACHES

A logical complement to the ethnographic approach detailed above is to conduct longitudinal observational studies on known individuals in the wild to document the ontogenetic trajectory of proposed socially learned behaviors. This has been done relatively infrequently, owing to the extremely high costs in time and money required to conduct long-term field studies and maintain the appropriate demographic records to reliably track individuals. However, as more long-term studies come to light across a variety of taxa, this approach has become more common. Below, we summarize key findings of developmental studies by taxonomic group before reviewing some overarching opportunities and constraints that may apply across taxa.

Fish

Although social learning is well documented among fish (reviewed in Brown & Laland, 2003), few studies have investigated social learning within a developmental context in these taxa. Rather than investigating the development of a particular skill, Chapman, Ward, and Krause (2008) investigated the role of group density during development in later foraging success in laboratory-housed guppies. When raised with a small number of conspecifics, guppies were quicker to locate food by following a trained adult guppy than were guppies raised in large groups. This counterintuitive finding is explained by the fact that guppies reared in the high-density condition were less likely to shoal with others and, therefore, were less likely to learn the benefits of social learning. Instead, fish reared in high-density situations may learn that conspecifics are to be viewed as competitors, rather than as potential sources of adaptive information. This finding suggests that at least for guppies, the early social environment may have an effect on the capacity for social learning, if not on the socially learned behaviors themselves.

Birds

Among birds, social learning has been shown to have an impact on the development of foraging behavior (re-

viewed by Lefebvre & Bouchard, 2003), including food handling or other foraging techniques (e.g., Cadieu, Winterton, & Cadieu, 2008; Göth & Evans, 2005; Holzhaider, Hunt, & Gray, 2010b; Kenward, Rutz, Weir, & Kacelnik, 2006), and learning of preferred foods or foods to be avoided (e.g., Benskin, Mann, Lachlan, & Slater, 2002; Nicol, 2004). Holzhaider, Hunt, and Gray (2010a, 2010b), for example, tracked the development of tool manufacturing by wild New Caledonian crows and reported that social learning plays at least a minor role in the acquisition of this skill among young birds. However, within the literature on avian social learning, the majority of developmental approaches have focused on vocal learning. For many song birds, the development of an individual's vocal repertoire is influenced by the songs heard as a young bird in the early days and weeks of life. Hearing the songs of conspecifics is critical for the normal development of this behavior, and in the absence of these opportunities at appropriate times, individuals usually fail to acquire a functional song repertoire (e.g., Kroodsma, 1978; Nottebohm, 1970). But whether the development of vocal communication in birds or other animals (e.g., vervet monkeys; Seyfarth & Cheney, 1986) can be placed in the same category as most examples of social learning has been debated (e.g., Galef, 1976; Shettleworth, 1998; Whiten & Ham, 1992). A better example of the role of social learning in bird song, perhaps, is the development, spread, and maintenance of vocal dialects observed in some populations (e.g., Kroodsma, Baker, Baptista, & Petrinovich, 1985; Marler & Tamura, 1962). Dialects result when individuals learn songs that are similar to those of conspecifics living in the same geographic region but distinct from those of conspecifics in other locations. The timing of exposure to different songs may also be critical to the development of an appropriate dialect. Cunningham and Baker (1983) exposed male white-crowned sparrows to their natal dialect early during the first 50 days of life and to an alternative dialect for the following 40 days. The majority of males learned and maintained the early dialect throughout their life, suggesting that in this species, the development of dialects within an individual and the sustainability of dialects in a population rely on early developmental experience during a critical learning period.

Mammals

Among mammalian taxa, the developmental approach has been applied with a variety of species, including rats (Galef, 2003), bottlenose dolphins (Sargeant & Mann, 2009), brown bears (Mazur & Seher, 2008), and chimpanzees (e.g., Inoue-Nakamura & Matsuzawa, 1997). The majority of these studies have focused on foraging behaviors, since synchronicity between adult and offspring feeding suggests an important role for social learning in terms of learning which foods are edible and/or preferred, as well as how to access food items that need processing. Likewise, the majority of transmission is vertical—that is, from mother to offspring, since mammalian mothers are typically the primary source of information for offspring during development.

Rodents. Among rats, the development of food preferences has repeatedly been shown to involve social learning. At weaning, young rats must learn quickly which foods are safe or palatable to eat, but relying on individual trial-and-error learning may have deadly consequences. As a result, young rats not only prefer to eat near others, but also develop preferences for foods that adults in their colony have eaten. In a foundational study, pups born to wild-caught adults who had previously learned to avoid foods that contained nonlethal toxins also learned to avoid those foods and ate only those foods that their mothers and other adults in the colony were eating (Galef & Clark, 1971). Subsequent studies, reviewed in Galef (1996, 2003), showed that social influences on food preferences may even occur prior to weaning and can persist through multiple generations, long after members of the original colony are removed. This set of studies illustrates the potential longevity and power of these early social-learning experiences on the development of food preferences in rodents.

Marine mammals. In a longitudinal study of wild bottlenose dolphin foraging traditions in Shark Bay, Australia, Sargeant and Mann (2009) examined the contributions of habitat heterogeneity and social information to the development of 13 different foraging tactics. The authors used multivariate techniques in an attempt to investigate ecological influences on foraging tactic development, thereby making a substantial effort to address prior criticisms that field studies do not do enough to control for ecological differences (see above). For three of the tactics, there was strong evidence of vertical social learning; calves were significantly more likely to develop these tactics if their mother displayed them. In contrast, horizontal social learning (from other conspecifics) did not contribute substantially to foraging tactic development, despite the highly social nature of this species. Indeed, other reports from cetacean field studies suggest that vertical transmission among matrilineal social groups may be the norm and may give rise to differences in habitat use and vocal behavior (e.g., Whitehead & Rendell, 2004) among groups.

Primates. In a recent review, Rapaport and Brown (2008) summarized and described the potential role of social learning in the development of foraging across the primate order. For prosimians, very little is known regarding the role of social- versus individual-based learning in the ontogeny of foraging, owing to a relative lack of study of these taxa. Among new world monkeys, examples abound (Rapaport & Brown, 2008), but perhaps the most intriguing is that of the complex stone tool use exhibited by wild capuchin monkeys while foraging on nuts. Through intensive observation of known individuals over the course of development of the behavior, researchers have documented the careful attentiveness of youngsters to proficient adults, the developmental trajectory of the behavior, and the different foraging traditions displayed by different capuchin populations (reviewed in Ottoni & Izar, 2008). Among the apes, there is the most data regarding chimpanzees, and several studies have now focused on offspring development of more complex, tool-assisted foraging techniques, such as nut cracking (Biro et al., 2003),

termite fishing (Lonsdorf, 2005), and ant dipping (Humle, Snowdon, & Matsuzawa, 2009), where there is strong evidence that social learning plays a key role in the development of these behaviors (see below). Similar evidence is beginning to come to light in orangutans as well, where Jaeggi et al. (2009) reported that immature individuals had a diet nearly identical to that of their mothers, despite considerable variation among those mothers. In addition, all immatures increased their frequency of observing their mothers when they performed more complex foraging behaviors, such as processing embedded fruit, lending support to the growing theoretical and experimental body of evidence that social learning should be employed as a task becomes more difficult (Boyd & Richerson, 1988; Kendal, Kendal, Hoppitt, & Laland, 2009; Laland, 2004).

Opportunities for “Natural Experiments”

In addition to characterizing the developmental trajectory of socially learned behaviors, opportunities have arisen to observe natural “experiments,” owing to circumstances that conceptually resemble the *two-action* experiments commonly used in the laboratory. In these experiments, observers are shown one of two different methods for completing a task (e.g., push or pull a knob), and if the observers more commonly produce the method that was demonstrated to them, social learning is presumed to have occurred (reviewed in Whiten & Ham, 1992). In the case of a field study, the analogy is two different conditions or categories of individuals. Sex differences in offspring development are one such categorical divide. For example, young chimpanzee females were more attentive to their mothers’ termite-fishing behavior and subsequently showed shorter acquisition times and higher proficiency than did male offspring. Daughters were also more likely than sons to match their mothers’ precise technique (Lonsdorf, 2005; Lonsdorf, Eberly, & Pusey, 2004). These differences occurred despite no observable differences in the way in which mother chimpanzees behaved toward male or female offspring (Lonsdorf, 2006). In tufted capuchins (Agostini & Visalberghi, 2005), youngsters exhibited sex differences in foraging development consistent with differences in diet shown in adults of the species. In particular, young males preferentially focused their attention on the feeding behavior of adult males and, subsequently, showed significantly more diet overlap with adult males than with adult females. Similarly, Perry (2009) has recently documented a sex difference in the development of fruit processing in wild white-faced capuchins. Of two potential methods for processing *Luehea candida* fruits, female offspring were significantly more likely to adopt the maternal technique than were males, although the underlying mechanisms remain a mystery, since differences in attentiveness were not detected.

Another example of a “natural” experiment impacting the ontogeny of foraging comes from black bears. Mazur and Seher (2008) studied free-ranging black bears at Yosemite and Sequoia National Parks for 11 years. Sows either reared their offspring in wild areas and, therefore, foraged on wild foods or reared offspring in developed areas and foraged on anthropogenic food sources. Cubs were then

followed after their yearling dispersal, when they sought out new territories independently from their mothers. The authors found a strong impact of maternal foraging style (wild vs. food conditioned), which significantly predicted the foraging style of cubs once they were independent (but see Breck et al., 2008, for an alternative approach). In this case, the results had important management implications, since managers could predict and plan ahead for potential problem bears on the basis of maternal tendency to forage on human food sources (for additional management implications of social learning, see Whitehead, 2010).

In a recent study of wild chimpanzee ant dipping, multiple conditions and categories of individuals were investigated (Humle et al., 2009). At Bossou, Guinea, chimpanzees dip at ant nests, which are high risk to offspring in terms of being bitten by ants, and at ant trails, which are lower risk. Mothers with young offspring (5 years old or younger) ant dipped significantly more at trails, which provided a less risky learning situation for both mothers and offspring, than at nests. Mothers also differed in the percentage of time spent ant dipping, and the offspring of more frequent dippers acquired the skill more quickly and were more proficient. Moreover, mothers and weaned offspring positively correlated in the percentage of time spent ant dipping and in their proficiency (Humle et al., 2009). As in the bottlenose dolphin study by Sargeant and Mann (2009) reviewed above, this study integrated ecological influences and social processes, while being able to compare and contrast different categories of mothers.

Developmental Constraints

Although there is now good evidence that social learning plays a key role in the ontogeny of some behaviors, there are both social and nonsocial constraints that must be incorporated into the conceptual framework of any social-learning study. The influence of age and/or maturation on the likelihood of acquisition is one such constraint. Inoue-Nakamura and Matsuzawa (1997) suggested that there exists a critical period for the learning of nut cracking by wild chimpanzees (between the ages of 3 and 5 years), beyond which exposure will not support acquisition. However, older individuals have acquired nut cracking in experimental settings (Hayashi, Mizuno, & Matsuzawa, 2005; Ross, Milstein, Calcutt, & Lonsdorf, 2010), so the importance of a critical period for the learning of such skills in the wild remains to be seen. Furthermore, Corp and Byrne (2002) described the ontogeny of foraging on *Saba florida* fruit in chimpanzees, which requires a significant amount of processing and manual dexterity, highlighting the interaction between the physical constraints of manual maturation and the social influences of synchronous feeding and food sharing. Such maturational constraints may also be present in the transmission of handclasp grooming in chimpanzees, a posture in which two individuals sit facing each other, holding outstretched arms overhead while grooming the armpit area of one another. Data from both wild and captive populations suggest that individuals must reach a certain age, or size, in order to perform this behavior effectively (Bonnie & de Waal, 2006; Nakamura,

2002). In terms of social constraints, if a skill requires exposure to a knowledgeable demonstrator to develop, the presence of appropriate and/or tolerant models is required. For example, Leca, Gunst, and Huffman (2007) reported that low rates of stone handling among some groups of Japanese macaques may be a result of low numbers of young adult models demonstrating the behavior. Finally, social systems that are less tolerant or particular aspects of the demonstrator or the learner may impact the likelihood of transmission, as described below.

SOCIAL CONSTRAINTS

Social System

Over 10 years ago, Coussi-Korbel and Fragaszy (1995) advocated paying closer attention to social context when conducting social-learning studies, arguing that

Within stable social groups, long-term social relationships develop, and dynamic social processes influence all aspects of life. Thus social learning takes place within a structured social context for many animals. It seems likely that the specific social context in which a group-living animal finds itself influences its opportunities for social learning, and perhaps also its propensity to learn certain things from certain individuals. This aspect of social learning has not received the formal attention it deserves. (p. 1441)

Another prediction from this work is that behaviors will spread more *evenly* in egalitarian societies and in a more skewed or asymmetric manner in despotic societies. Similarly, van Schaik, Deaner, and Merrill's (1999) socioecological model for the evolution of material culture consisted of four criteria that determined the invention and propagation of an extractive foraging behavior (e.g., chimpanzee termite fishing): (1) ecological opportunities, (2) motor dexterity, (3) cognitive abilities, and (4) social tolerance, highlighting the importance of taking social factors into account. Fortunately, a host of new methods are currently being used to understand and quantify social networks within animal groups (see Wey, Blumstein, Shen, & Jordan, 2008, for a recent review). Building on this work, theoretical, statistical, and modeling approaches are beginning to identify not only the existence of social learning (Kendal, Kendal, et al., 2009), but also how variation within a social network may affect transmission (see Franz & Nunn, 2009, 2010; Hoppitt et al., 2010).

Experimental and observational data have emerged that validate some of the theoretical work. For example, Drea and Wallen (1999) found that subordinate rhesus monkeys that had learned a task would perform it only when in a group with other subordinates and would not perform it in the presence of dominant individuals, suggesting that the social setting may inhibit knowledge expression, as well as acquisition. Following the socioecological model of cultural evolution described above, van Schaik (2003) compared the size of particular chimpanzee communities' tool kits in relation to a measure of social tolerance (percentage of time spent in parties) and found a strong

positive correlation. In a parallel analysis for orangutans, he found that within-group variation in the degree of tool use was correlated with exposure to other individuals in a relaxed foraging context; that is, high exposure correlated with more tool use. More recently, Lonsdorf, Ross, Linick, Milstein, and Melber (2009) reported that a lack of social tolerance in naturally housed gorillas likely prevented some individuals from learning (or expressing knowledge of) a tool use task, whereas higher levels of affiliation in a group of chimpanzees likely contributed to most individuals' acquiring the same task. Similarly, in cooperatively breeding jackdaws, individuals were equally attentive to the food-related behavior of conspecifics, in comparison with facultatively social ravens, which were more selective and attended more strongly to "friends" (Scheid, Range, & Bugnyar, 2007). In summary, a key first step to studying and identifying social learning in natural contexts is a thorough understanding of the social structure of the target species and/or individuals. The next step is to understand social constraints as they impact individuals within their social structure.

The Influence of Social Networks

Early theoretical models of social learning typically assumed that social interactions occur at random within a group of individuals; thus, these models critically ignored the effects that social variables can have on social learning. The majority of earlier empirical work on social learning followed this line of thinking, with few studies accounting for the relationship between observers and demonstrators (de Waal, 2001; de Waal & Bonnie, 2009). In contrast, recent developments in the theoretical literature suggest that the nature of the relationship between individuals, including variables such as familiarity, kinship, and social affiliation, as well as characteristics of the demonstrator, including physical characteristics, social rank, age, and skill proficiency, can critically affect the likelihood that observers will copy the behavior of another individual (Coussi-Korbel & Fragaszy, 1995; Henrich & Gil-White, 2001; Laland, 2004). Below we review some of the evidence in support of these ideas.

One approach for determining the role that the social relationship between individuals has on social learning is to track the spread of a behavior among a group of individuals for which social affiliations are well known. As was previously mentioned, this is difficult to accomplish in wild populations and, sometimes, surprisingly difficult in studies of captive animals (e.g., Smith, King, & West, 2002). Nevertheless, a few illustrative examples do exist. Bonnie and de Waal (2006) found that the degree of affiliation between any given pair of individuals in a captive chimpanzee group influenced the development of handclasp grooming within that pair. This finding is not entirely unexpected, given that individuals who have a strong affiliation likely groom each other frequently, and the handclasp posture may seem to be an obvious next step. But grooming and other affiliative behaviors did not always lead to handclasp grooming among even the most affiliated pairs, although it was much more likely to

be observed among these individuals than among others (Bonnie & de Waal, 2006).

Sweet potato washing, a unique food-handling behavior shown by Japanese macaques, is reported to have spread first among age mates and the mother of the inventor of this behavior, and only later to individuals whose interactions with the first washer were less frequent or socially significant (de Waal, 2001; Kawai, 1965). In other troops of Japanese macaques, the spread of stone-handling techniques is also thought to be transmitted along affiliative lines (Leca et al., 2007). However, in a recent study on starlings (Boogert, Reader, Hoppitt, & Laland, 2008), association patterns did not predict the spread of solving a newly introduced task. Rather, individual characteristics, such as rank, learning propensities, and object neophobia, were most predictive of latency to solve the task, suggesting that care must be taken not to overgeneralize the importance of association patterns across species with different social systems (see above).

Characteristics of the Demonstrator–Observer Dyad

These findings, and the theories that inspired and support them, have led to a surge in experiments in which the nature of the social relationship within demonstrator–observer pairs has been directly manipulated within a social-learning paradigm. In a study of social learning among captive brown capuchin monkeys, subjects were paired with demonstrators of varying social affiliations; some pairs were characterized as affiliative, others as generally agonistic (de Waal & Bonnie, 2009). Monkeys were more likely to copy the choices made by a positively affiliated demonstrator, in comparison with an agonistic partner, but only when the demonstrator was rewarded for its efforts and the subject was not. If both monkeys could retrieve a food reward, the nature of the relationship between the two individuals had no significant effect.

Other work has concentrated on one or more specific variables within a demonstrator–observer relationship, including familiarity (Cadieu & Cadieu, 2004; Galef & Whiskin, 2008; Swaney, Kendal, Capon, Brown, & Laland, 2001) and genetic relatedness (Schwab, Bugnyar, Schloegl, & Kotrschal, 2008). With respect to familiarity, attending to and copying the behavior of a familiar individual may be advantageous, in that familiar individuals are more likely to have acquired behavior in an environment shared by the observer, so that the learned behavior is likely to yield the same benefits for the observer. Demonstrator–observer familiarity enhanced the rate at which guppies learned a foraging task (Swaney et al., 2001), but familiarity had no effect on the rate and frequency of interactions of young canaries with a complex food resource (Cadieu & Cadieu, 2004). The effect of demonstrator–observer genetic relatedness may be equally equivocal. Whereas Valsecchi, Choleris, Moles, Guo, and Mainardi (1996) found that gerbils acquired food preferences through social learning only when demonstrators were familiar or genetically related to observers, Galef et al. (1998) showed that unfamiliar and/or unrelated demonstrators had as much influ-

ence as familiar/related demonstrators. These conflicting findings, as Galef et al. pointed out, may be a product of methodological differences in the timing of the interaction between individuals, rather than familiarity, and highlight the need to pay close attention to the methodologies used across studies to test these effects. In contrast, genetic relatedness has been shown to have a positive influence on social learning among ravens, such that young male ravens were more likely to copy the object manipulation and caching behavior of a sibling than of a familiar nonsibling (Schwab et al., 2008). Given these and other conflicting findings, further investigation into the influences of familiarity and relatedness is warranted. Moreover, care should be taken to understand the potential impact of these factors when designing social-learning studies.

Unfortunately, this type of research is limited to species that tolerate the presence of an unknown or unfamiliar individual well, species for which genetic relatedness is known and recognized, and/or species in which social learning can occur in the absence of close or direct physical or visual contact. Until recently, this excluded, among others, most primates. However, in two recent studies, chimpanzees (Price, Lambeth, Schapiro, & Whiten, 2009) and colobus monkeys (Price & Caldwell, 2007) demonstrated the ability to learn a task by watching a video of conspecifics. In addition, marmosets appear able to interact in an experimental situation with unfamiliar individuals (Burkart, Fehr, Efferson, & van Schaik, 2007), suggesting that these approaches may allow for more control and investigation of social variables in future studies.

Demonstrator Characteristics

Irrespective of the genetic and/or social relationship between individuals, recent developments in the theoretical literature also suggest that characteristics of the demonstrator critically affect the likelihood that observers will copy the behavior of another individual (Coussi-Korbel & Fragaszy, 1995; Henrich & Gil-White, 2001; Laland, 2004). In line with this, Laland suggested a number of *who* strategies that, when other social and individual factors are controlled for, dictate the circumstances under which individuals learn from others and, more specifically, predict from whom individuals will learn. These *from whom* variables include sex (e.g., Cadieu, Fruchard, & Cadieu, 2010; Katz & Lachlan, 2003), age (e.g., rats, Galef & Whiskin, 2004; guppies, Amlacher & Dugatkin, 2005; elephant seals, Sanvito, Galimberti, & Miller, 2007), rank (e.g., Bonnie et al., 2007; Nicol & Pope, 1999), expertise (Ottoni, de Resende, & Izar, 2005), and prestige (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). Guppies, for example, tend to copy the mate choice decisions of older males more so than those of younger males (Amlacher & Dugatkin, 2005), whereas chickens seem to be influenced by the social status of demonstrators within the flock (Nicol & Pope, 1999). In wild vervet monkeys, van de Waal, Renevey, Favre, and Bshary (2010) presented *artificial fruits* to social groups with either a dominant female or a dominant male as the demonstrator and found that groups with female demonstrators showed higher par-

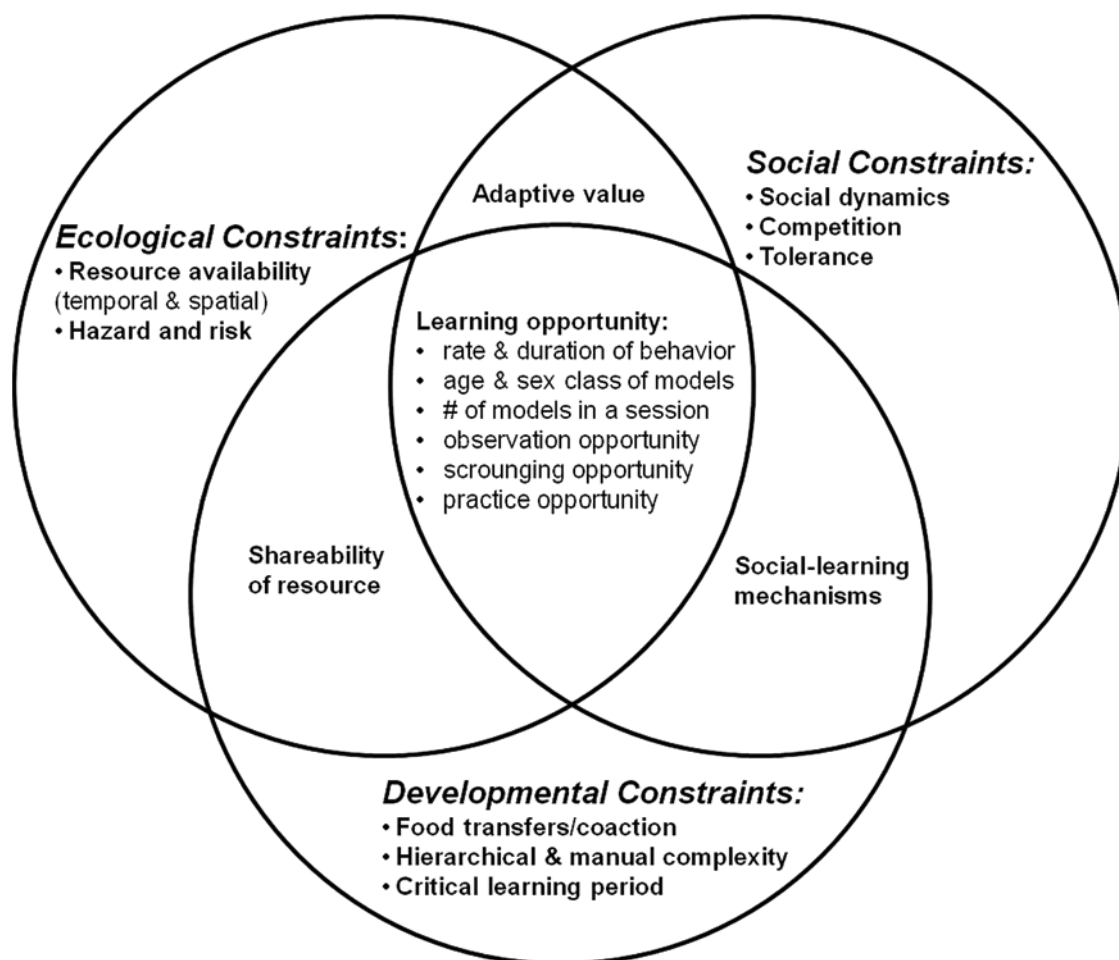


Figure 1. Conceptual schematic of the variables influencing ecological, social, and developmental constraints on the transmission and maintenance of cultural variants. From “How Are Army Ants Shedding New Light on Culture in Chimpanzees?” by T. Humle, in *The Mind of the Chimpanzee: Ecological and Experimental Perspectives*, edited by E. V. Lonsdorf, S. R. Ross, and T. Matsuzawa, in press, Chicago: University of Chicago Press. Copyright 2010 by University of Chicago Press. Reprinted with permission.

ticipation and correct responses. A review of many other recent discoveries in this area has been provided by Kendal, Coolen, and Laland (2009).

As a result of these and other observations, there has been a shift in the design of experimental studies toward carefully chosen conspecific models, in order to facilitate social learning. For example, using a transmission chain paradigm in which an observer becomes a demonstrator for the next individual in line, both Horner, Whiten, Flynn, and de Waal (2006) and Dindo, Thierry, and Whiten (2008) argued that successful transmission of behavior along the chain was, at least in part, a result of the order of the individuals in the chain itself. In these studies, chimpanzees (Horner et al., 2006) and capuchin monkeys (Dindo et al., 2008) learned to retrieve a food reward from an opaque container, using the method demonstrated by the individual ahead of them in the chain. Social learning in these cases was facilitated by the fact that the demonstrator at each point along the chain outranked the observer and, thus, could maintain control of the apparatus during the

demonstration phase. However, the dyadic relationship was tolerant enough that the observer was willing to approach and observe the demonstrator. In fact, in a minority of cases, the chain temporarily broke down when an observer was unwilling to approach and observe a particular demonstrator. When the observer was subsequently paired with a different demonstrator, with whom it presumably had a more positive relationship, the chain was reinitiated (Horner, in press). In these studies, the experimental methodology was carefully planned on the basis of a rich understanding of social relationships among the group and on preliminary tests for cofeeding tolerance. As such, these studies highlight how careful attention to social relationships is necessary in both wild and experimental studies of social learning.

Conformity

Despite the myriad of potential influences of the specific dyadic relationships and of individual demonstrator or learner characteristics, new research suggests that

these may be overridden by social species' motivation to conform. Conformity is likely widespread among the animal kingdom, but perhaps, as Hoffer (1955) suggested, this may be truer for humans than for any other species, who, "when free to do as they please . . . usually imitate each other" (p. 17). Support for Hoffer's claim comes from numerous examples of fashion or behavioral fads that spread through unaffiliated and unknown individuals around the world (e.g., Bentley, Hahn, & Shennan, 2004; Herzog, Bentley, & Hahn, 2004). But conformity to cultural norms is not limited to humans. Whiten, Horner, and de Waal (2005) found that despite discovering an equally successful alternative solution to a foraging problem, captive chimpanzees adopted the technique used by the majority of individuals in their social group. Similar results have also been reported for captive capuchin monkeys (Dindo, Whiten, & de Waal, 2009) and fish (Day, MacDonald, Brown, Laland, & Reader, 2001). In these cases, conformist desires might motivate the adoption of socially learned behaviors, and additional work has demonstrated that conformity might be particularly powerful among naive individuals who lack individual experience (Kendal, Coolen, & Laland, 2004). However, it has also been argued that these and other claims for conformity among nonhuman animals are better interpreted as simply evidence that individuals copy the most frequent form of behavior present, rather than as evidence for conformity defined as an *exaggerated* tendency to adopt the most frequent behavior (Eferson, Lalive, Richerson, McElreath, & Lubell, 2008). More empirical work in this area is required to untangle the subtle yet potentially important differences between frequency-dependent social learning and conformity within animal groups.

IMPLICATIONS FOR IDENTIFYING SOCIAL LEARNING IN THE WILD AND UNDERSTANDING CULTURAL EVOLUTION

Above, we have explored a host of methodological approaches, considerations, and constraints as they apply to identifying social learning in natural contexts. After reviewing the above, readers may be tempted to throw their hands up in surrender and choose a different field of study. Field studies are criticized for lack of tight controls, and captive experiments are derided for lacking external validity. Developmental studies help to fill some of the gaps, as we have described above, but are logistically and financially challenging to carry out. New theoretical approaches are advancing social-learning studies in impressive ways but need corresponding experimental data to validate the predictions. Moreover, the difficulties of accounting for, controlling, and/or testing the impact of genetics, environment, experiences during ontogeny, social systems, rank relationships, and so forth may seem insurmountable at first glance. However, we believe the contrary—that the study of social learning is reaching a critical *tipping point* , where numerous approaches, quan-

titative tools, and species undergoing study are coalescing so as to allow us to study the intricacies of cultural evolution in more detail than ever before.

In a recent case study report on chimpanzee ant dipping as a culture behavior, Humle (in press) provided a useful conceptual model that attempts to integrate how ecological, developmental, and social influences and constraints may shape cultural evolution (see Figure 1). We have attempted to briefly review many, but not all, of these factors in this contribution, and we refer the reader to Humle for a more detailed description as it applies to chimpanzee tool use. The main point we wish to emphasize is that although the social learning and subsequent "culture" picture may seem quite complicated, it is precisely this complexity that likely shaped human cultural evolution. Like chimpanzees (and many other species, as reviewed above), humans exist within complex and varied social systems, across different ecologies, with individual differences in qualities such as temperament, motivation, and so forth. A unifying theory of cultural evolution will necessitate a combination of the approaches above, overlaid on the recognition of humans and animals as lying on a continuum of social learning and cultural capacity. Lastly, our ability to study how culture has evolved and is transmitted and manifested throughout the animal kingdom will depend largely on our ability to conserve and care for the animals we study in both wild and captive settings (see Whitehead, 2010). The alarming loss of species and their habitats over the past century means that some critical referential information for cultural evolution may be lost forever. As scientists who study these species and their potential cultural capacities, it is our duty and in our own best interest to conserve and protect those that remain.

AUTHOR NOTE

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