Chapter 19

THE COMPARATIVE PSYCHOLOGY OF SOCIAL LEARNING

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The last 3 decades have seen an extraordinary increase in studies of social learning in nonhuman animals and humans. The relevant literature is unusual in the range of backgrounds of authors making substantial empirical or theoretical contributions to our understanding of social influences on the acquisition of behavior. However, despite the diversity in the academic disciplines of those studying social learning, there has been general agreement as to the subject matter of the field. Indeed, we know of no one working in the area who would take exception to defining social learning as "learning that is influenced by observation of, or interaction with, a conspecific or its products" (Heyes, 1994, p. 207).

As might be expected given the breadth of interests of those studying social learning in animals and the resultant scatter of relevant publications across specialized journals in many disciplines, the need for reviews of work in the area was recognized early in its history, and assessments of progress in social learning in general and in subareas of the field have been frequent (see Appendix 19.1). The present discussion builds on its predecessors, but differs in that, consistent with the topic of this handbook, we explicitly consider the study of social learning as a branch of comparative psychology.

The first challenge to such an approach results from the considerable diversity of opinion concerning the defining features of this field of inquiry (reviewed in Demarest, 1980). Historically, the term *comparative psychology* has often been used in a rather general way to refer to the scientific study of behavior and cognition in nonhuman animals. This usage, however, led Konrad Lorenz to opine "I strongly resent it . . . when an American journal [the *Journal of Comparative and Physiological Psychology*] masquerades under the title of 'comparative' psychology, although to the best of my knowledge, no really comparative paper ever has been published in it" (Lorenz, 1950, pp. 239–240).

Lorenz and other more biologically oriented researchers (e.g., Hodos & Campbell, 1969) advocated a comparative psychology focused on studies of similarities and dissimilarities in homologous behavioral traits of closely related species. Indeed, when Romanes (1884), Darwin's protégé in matters behavioral, introduced the term comparative psychology into the modern scientific literature, he used the term in Lorenz's sense, proposing that comparative psychology should be modeled on comparative anatomy, focused on comparisons between closely related species and tracing the evolution of morphological traits:

> In the family of the sciences, Comparative Psychology may claim nearest kinship with Comparative Anatomy; for just as the latter aims for the scientific comparison of the bodily structures of organisms, so the former aims at similar comparisons of their mental structures. (Romanes, 1884, p. 5)

Romanes, however, recognized that comparisons of closely related species had to be preceded by examination of the "mental structures" of individual species. "When this analysis or dissection has been completed . . . the next object is to compare

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with one another all the structures which have thus been analyzed" (Romanes, 1884, p. 5). The results of such comparisons can be used "to [classify] all the structures thus examined . . . [though] in actual research these three objects are prosecuted not successively, but simultaneously" (p. 5).

In sum, in Romanes's view, comparative psychology involves three synergistic activities to be pursued simultaneously: (a) description of the mental structures of individual species, (b) comparison of such structures between closely related species, and (c) classification of similarities and differences. Although today we would be more likely to speak of cognitive processes inferred from behavioral observations than of mental structures and classification is seen as less central to scientific progress than it was in Romanes's day (when physics and taxonomy were considered to be the premiere sciences), the considerable diversity of current work on social learning in animals falls rather neatly into Romanes's scheme.

In the first part of this chapter, we use work on social learning published from January 2012 to December 2014 to determine whether students of social learning have overcome a suite of scientific "sins" of which the broader field of comparative psychology has, historically, been accused. Next, we briefly discuss classifications of social learning to provide a framework within which to consider teaching: A behavior that, like imitation, has been considered a uniquely human characteristic but is now viewed as part of the behavioral repertoire of nonhuman animals as well. Finally, we address Romanes's third goal, direct comparison of social learning in closely related species, focussing where the literature is richest, on comparisons of humans with other apes. This chapter is complemented by Chapter 20 of this volume, which focuses on the larger-scale phenomena of tradition and culture that are crucially dependent on social learning.

CONTRIBUTION OF STUDIES OF SOCIAL LEARNING TO COMPARATIVE PSYCHOLOGY

Classic comparative psychology has been criticized (see Lockard, 1971) for focusing on (a) a very limited range of species (Beach, 1950), (b) domesticated rather than wild animals, (c) too few and biologically irrelevant behaviors, (d) laboratory rather than field studies, and (e) the topic of learning at the expense of other factors important in behavioral development, as well as (f) working with a naive view of phylogenetics on the basis of the medieval *Scala Nature* rather than Darwinian evolution (Hodos & Campbell, 1969). We shall not elaborate on these criticisms here. Our review of the current literature on social learning clearly shows that today comparative psychologists studying social learning are far from guilty of these sins against biology, which were once attributed to the field.

We have examined all experimental papers on social learning cited in Web of Knowledge during the years 2012–2014 and listed the species and behaviors studied, as well the context (laboratory or field) in which research was conducted. A summary of the results of this overview are presented in Table 19.1. Citations of the reviewed publications, criteria for their selection, and the detailed table summarized in the text are available in Appendix 19.2.

As can be seen from Table 19.1, even in this snapshot of 36 months of publications, at least 104 research groups reported working with 66 species. Although amphibians, reptiles, and molluscs were clearly underrepresented, possibly because they do not often exhibit interesting examples of social influence on learning, a substantial number of vertebrate species and several different insects were subjects of study. Similarly, wild (55) and domesticated (11) species were well represented in the contemporary social-learning literature, with the standard laboratory rodents, so overrepresented in classic comparative psychology (Beach, 1950), playing a relatively small, though important, role.

Studies of social learning in avian species are more likely to be conducted in free-living than in captive populations, whereas terrestrial mammals and fish have been far more frequently studied in the laboratory than in the field. These data are consistent with the view that the relative ease of studying territorial, diurnal animals living in social groups, rather than intellectual bias, has played the major role deciding whether to study social learning in laboratory or natural circumstances.

TABLE 19.1

Summary of Experimental Publications, 2012–2014

Class	Research groups	Species	Wild/domestic	Captive/free	Behaviors
Primates	29	10	10 wild	4 free, 4 both	16
Mammals	31	20	15 wild	9 free, 1 both	22
Birds	17	15	13 wild	12 free	15
Fish	16	12	9 wild	0 free	7
Insects	7	5	4 wild	0 free	5
Other	4	4	4 wild	0 free	3
Totals	104	66	55 wild	25 free, 5 both	43

Note. Counting behaviors is necessarily somewhat subjective. The dependent variables used in the papers summarized in the table include preferences for foods, feeding sites, mates, and nest sites and the avoidance of predators, brood parasites, and biting insects.

Further, although work on social transmission of arbitrary laboratory operants (14 research groups) still occurs, primarily in mammals, the overwhelming majority of studies in all classes are of behaviors that animals might be expected to display in natural circumstances or are recognizable analogues of such behaviors adapted to captive study.

Because many research groups have become involved in studies of particularly promising phenomena, some areas, such as song learning in birds (for a recent review, see Catchpole & Slater, 2008; see also Volume 1, Chapter 26, this handbook), transmission of food preference in rodents, and imitation in chimpanzees (*Pan troglodytes*), have received inordinate attention. However, despite such focus, the number of behaviors investigated remains high. For example, studies of social influence on avian learning involved migration, homing (see Chapter 22, this volume), brood-parasite avoidance, nest-site selection, feeding-site selection, mate-choice, clutch size, tool use (see Chapter 30, this volume), social skills, and the spread of feeding innovations (see Chapters 20 and 28, this volume). In fish, social influences on predator avoidance, mate-choice (see Volume 1, Chapter 37, this handbook), and various aspects of foraging predominated, whereas insects were most frequently studied as sources of information on feeding-site selection, egg-deposition-site preference and predator avoidance (see Volume 1, Chapter 40, this handbook), though studies of laterality (see Volume 1, Chapter 27, this handbook) and spatial learning (see Chapter 21, this volume) in insects were also reported.

No simple enumeration of species and behaviors investigated can provide much insight into work in a field. Next, we describe four illustrative areas of research where progress has been particularly impressive, involving such subjects as a mammal, a bird, a fish and an insect.

Social Transmission of Information Concerning Distant Foods: Rats and Mice

Currently, the most heavily researched area in studies of social influence on the acquisition of behavior in nonprimate mammals involves the social transmission of food preference (STFP). The following is a now standard paradigm, originally developed as a laboratory analogue of a situation assumed to occur whenever a member of a central-place foraging species discovers and eats a food before returning to the harborage site it shares with others of its species (Galef & Wigmore, 1983): (1) A “demonstrator” animal first eats one of two diets, then, (2) in the absence of food, interacts briefly with a naive conspecific “observer,” and finally (3) chooses, in isolation, between the two diets.

Invariably, the preferences of observer rodents (*Rattus norvegicus*) for the food that their respective demonstrators have eaten is substantially enhanced, and such effects are powerful and long-lasting, essentially undiminished a month or more after a demonstrator and observer interact (Clark, Broadbent, Zola, & Squire, 2002; Galef & Whiskin, 2003). STFP has been reported in many social, central-place foraging mammals from hyenas (*Crocuta crocuta*; Yoerg, 1991) to bats (*Carollia perspicillata*; Ratcliffe & ter Hofstede, 2005). Analyses of the sensory basis of such information transmission shows that the breath of a demonstrator rodent carries information allowing an observer (whether conspecific or human) to identify the food that the demonstrator had eaten (see Chapter 4, this volume), and equally important, a contextual cue that an observer has to experience at the same time that it experiences the diet-identifying cue, if exposure to the diet-identifying cue is to alter the observer's subsequent food preferences. Simple exposure to a diet by sniffing or eating has little effect on subjects' subsequent food selection.

Rodent breath contains several sulfur compounds, the most concentrated of which, carbon disulfide (CS_2), acts together with a food odor, as does the presence of a demonstrator, to produce changes in observers' food choices. For example, naive observer rats (*Rattus norvegicus*) or mice (*Mus musculus*) that interact with a piece of cotton batting dusted with food and moistened with CS_2 subsequently show as strong a preference for that food as do naive observers that interact with an anesthetized conspecific demonstrator dusted with the same food. Observers interacting with a piece of cotton batting dusted with a food and moistened with water showed no increase in preference for the food with which the cotton batting was dusted (Galef & White, 1988; Munger et al., 2010).

Much is now known of the sensory basis of sensitivity to CS_2. A small percentage of receptor neurons in the olfactory epithelium of mice (GC-D receptors) express guanylyl cyclase, and such GC-D receptors respond vigorously only to biologically relevant concentrations of CS_2 and a few related compounds (Leinders-Zufall et al., 2007). Homozygous gene-targeted mice with disruptions in the transmission cascades of their GC-D receptors fail to show an enhanced preference for foods, whether experienced on the breath of a demonstrator mouse or on a piece of cotton batting moistened with CS_2. By contrast, the STFP of heterozygous observer control mice with intact GC-D receptors are unimpaired (Munger et al., 2010).

STFP requires not only detection of olfactory stimuli, but also storage and utilization of memories of those stimuli. Work in several laboratories (e.g., Alvarez, Lipton, Melrose, & Eichenbaum, 2001) provided evidence that the hippocampus plays an important role in initial processing of STFPs, with longer-term memories residing in the orbitofrontal cortex. More recently, Lesburguères et al. (2011) used the absence of interactions among numerous STFPs in a single observer (Galef, Lee, & Whiskin, 2005) to further explore the interplay of hippocampus and cortex in early processing and later storage of STFPs. Contrary to the prevailing view that only the hippocampus is involved in early processing of memories (see Volume 1, Chapter 25, this handbook), Lesburguères et al. (2011) found that long-term memory was not established if the function of cortical structures was inhibited during the first week after an observer mouse interacted with a demonstrator. The finding was interpreted as showing that when an observer interacts with a demonstrator, specific neurons in hippocampus and cortex are allocated to that memory, and this subset of "tagged" neurons is necessary for later dialogue between hippocampus and cortex needed to establish long-term memory.

Perhaps the most surprising recent finding with respect to STFP is that it occurs even if observer and demonstrator are unconscious while interacting (Nicol, Sanchez-Andrade, Collado, Segonds-Pichon, & Kendrick, 2014). It has long been known that observers acquire a STFP from an unconscious demonstrator (Galef & Wigmore, 1983). However, the rather extraordinary finding that unconscious observer mice acquire a preference for a diet when exposed to an anesthetized demonstrator, but not when exposed to the diet alone (Burne, Johnston, Wilkinson, & Kendrick, 2010), promises extraordinary progress in understanding STFP and general effects of experience on preference development.

Advances in analysis of STFP have been ecological as well as neuroanatomical. For example, O'Mara, Dechmann, and Page (2014) working with a tropical, central-place foraging, frugivorous bat (*Uroderma bilobatum*) looked at individuals who had interacted simultaneously with two conspecific demonstrators, one previously fed a flavored food and the other with a different food placed on its fur.

When subsequently offered a choice between the two foods, observer bats preferred the food the demonstrator had eaten to the food on the demonstrator's fur. Discrimination between food cues carried on breath and on fur could lead bats to attend to particularly informative social cues. Ingested food has been eaten, whereas food on fur may have been contacted inadvertently.

Social Transmission of Experimentally Induced Behavioral Innovations: Great Tits

Two recent technical developments, the first statistical and the second a method for automatic, simultaneous tracking of the positions of members of free-living populations promise a revolution in field studies of social learning. Network-based diffusion analysis (NBDA), predicated on the assumption that propagation of behavior is more likely between individuals that spend time close to one another than between individuals that rarely associate, allows statistical detection of social learning in a population once its social structure has been determined (Hoppitt & Laland, 2013; see also Chapter 20, this volume). The combination of automated determination of association matrices using passive integrated transponders (PIT tags; Krause et al., 2013) and NBDA and other statistical methods (Hoppitt & Laland, 2013) for revealing correlations between network structure and the diffusion paths of behaviours through populations promises a revolution in field and laboratory studies of social learning.

NBDA can be used in either laboratory or field work (e.g., Hoppitt & Laland, 2013), not only to detect the involvement of social learning in the diffusion of behavior through populations, but also to identify particular learning mechanism involved in diffusion of a behavior, their relative strengths, and durations of action. Here, we discuss only a relatively simple application of NBDA. Aplin et al. (2014) have recently used an automated data collection system in conjunction with PIT tags and NBDA to describe the spread and persistence of behaviors introduced into populations of free-living great tits (*Parus major*), whose social network structure had been independently determined. Aplin et al. (2014) captured and trained two birds from each of five flocks of PIT-tagged birds to push the door of an automated feeder to either left or right to gain access to food. The authors traced the spread of introduced behaviors through these five populations and the three control populations without trained demonstrators.

Members of the five experimental flocks learned to open the puzzle box far more rapidly than members of the three control flocks and invariably used the same action (pushing the door to left or right) introduced into their flock. Year-long adherence to the introduced behaviors was seen in all five experimental flocks despite many individuals in each flock independently discovering the alternative action to acquire food and replacement of 60 percent of each flock by new recruits over the winter months. Most important, social structure predicted the path of diffusion of the introduced behaviors, with transmission rate between individuals linearly related to the frequency of association among individual flock members.

Social Influences on Mate Choice: Guppies and Mollies

Deciding which of several potential partners would make the better parent for one's offspring requires allocation of resources to evaluation of potential partners that might more profitably be directed to alternative activities. Copying someone else's choice ensures doing no worse than one's model without incurring the cost of evaluation and might be particularly valuable to young copying choices of older, more knowledgeable individuals.

A considerable literature indicates that female mammals, birds, and fish may show an increased preference for males they have seen court or mate with another female (for reviews, see Mery et al., 2009; Vakirtzis, 2011; see also Volume 1, Chapter 37, this handbook). In the first of such experiments, Dugatkin (1992) studied social influences on mate choices of female guppies (*Poecilia reticulata*), descendants of animals caught in the streams of Trinidad where wild guppies select partners and breed under conditions allowing observation and copying of one another's mate choices. In Dugatkin's laboratory, focal female guppies simultaneously watched one of two size-matched target males court another female (a model) while the other male remained alone. Each focal female was then released to choose between her target males. Seventeen of 20 focal females spent more time with the target male they had seen court a model female than with the target male they had seen alone.

Although such data are consistent with the hypothesis that female guppies copy one another's mate choices, they are open to alternative interpretations. For example, female guppies, members of a species that shoals in natural habitats, might prefer a location where they have previously seen two fish, to a location where they have seen only one (see Chapters 25 and 26, this volume). Also, the behavior or appearance of a male who has recently courted might be more attractive than those of a male who has not. Dugatkin's (1992) further experiments excluded a number of such plausible accounts of the increased affiliation of females with males they had observed courting, leading to the conclusion that focal females were copying the apparent choices of model females.

Evidence of mate-choice copying in fish is not confined to the laboratory. Witte and Ryan (2002) used a procedure analogous to that which Dugatkin (1992) had used to study social influence on the mate-choices of female guppies to investigate mate-choice copying in wild sailfin mollies. Witte and Ryan found that sailfin molly females (*Poecilia latipinna*) preferred to affiliate with males previously observed courting and that such enhanced association was, as Dugatkin found with guppies, not simply a consequence of mollies' tendency to shoal.

In natural environments sailfin mollies shoal with Amazonian mollies. Amazonian mollies (*Poecilia formosa*) are unusual in that although sperm is required to initiate their embryogenesis, inseminating males do not contribute genetic material to a female's eggs. Perhaps even more surprising, the sperm that initiates embryogenesis in female Amazonian mollies comes from mating with male sailfin mollies, although as noted previously, these males do not contribute genetic material to female Amazonian mollies' offspring.

It would seem a waste of time and energy for male sailfin mollies to court and inseminate heterospecific females who will not pass their genetic material on to future generations. However, Schlupp and Ryan (1996) have shown that a male sailfin molly becomes more attractive to conspecific females after they have seen him mate with an Amazonian molly. Thus, a superficially maladaptive behavior in male sailfin mollies is sustained by a tendency of female sailfin mollies to copy heterospecific females' mate choices. Social influences on mate choice are clearly more than a laboratory curiosity.

Social Influences on Choice of Feeding and Egg-Deposition Sites: Drosophila

Some of the earliest, and surely some of the strongest, evidence of social learning in any species is that provided by von Frisch (1967) and generations of students studying communication among honey bees (see Volume 1, Chapter 30, this handbook). Unfortunately, that work has not been well integrated into the literature on social learning, possibly because early in the 20th century, when von Frisch initiated his study of pheromonal and dance-language communication in honeybees (*Apis mellifera*), social learning did not exist as a coherent field of inquiry to which studies of honeybee communication could contribute. Consequently, work on honeybee communication, like work on bird-song learning (also well developed before studies of social learning had been integrated into a coherent field; see Volume 1, Chapter 26, this handbook), has proceeded not only very successfully, but also essentially independent of other contributions to the understanding of social learning in animals. Only in the last decade have studies of social influences on bumblebee (*Bombus terrestris*) foraging, orientation in ants (*Formicidae sp.*; see Chapter 22, this volume), and preferences of fruit flies (*Drosophila melanogaster*) brought work with insects into the main stream of the social-learning literature. (e.g., Leadbeater & Chittka, 2009; Dukas, 2010). Although studies of social influences on insect behavior are recent, intriguing findings, some with considerable potential for neurogenetic analyses of the physiological substrate of social learning are already available.

In natural environments, fruit flies aggregate in response to odors of ripe fruit and an aggregation pheromone released by adults at sites where they feed and lay eggs. In the laboratory, female fruit flies copy mate choices of others and are susceptible to social influences when selecting oviposition sites.

Reminiscent of STFP in Norway rats, Battesti, Moreno, Joly, & Mery (2012) have found that female fruit flies that have interacted in a neutral arena with a female that had laid her eggs on a scented medium subsequently preferred to deposit eggs on media with that scent. Preference acquisition required female flies to experience substrate cues on a conspecific; simple exposure to the substrate itself did not have a similar effect. Further, as in Norway rats (Galef & Aleen, 1995), socially transmitted preferences in fruit flies supported a local tradition with a socially learned preference passing from one generation to the next.

Sarin and Dukas (2009) showed that female fruit flies that experience a novel food together with other females that have laid eggs on that food subsequently show a greater probability of laying their own eggs on similar substrate than females that experienced the novel food alone. Further, female fruit flies are not only strongly attracted to food substrates previously occupied by larval fruit flies, but also subsequently prefer odors associated with such substrate. Increased duration of exposure to a substrate odor resulting from attractiveness of larval odor is entirely responsible for this change in preference (Durisko, Anderson, & Dukas, 2014).

Conclusion

The large corpus of recent studies enumerated in Table 19.1 and the sample of studies described previously involve a broad range of species, wild and domesticated, and biologically important behaviors studied in laboratory and field work. Gradual movement toward study of house mice, zebrafish (*Danio rerio)* and drosophila, species that for decades have served as model systems in the biological sciences, suggests that instances of social learning will soon be subject to sophisticated neurogenetic analyses and such integration of comparative psychological and biological approaches to studies of social learning promises a bright future for the field.

TEACHING: AN EXAMPLE OF ANALOGICAL CLASSIFICATION

Some outsiders to the field of social learning, especially those with a primary interest in functions rather than mechanisms of behavior, have found the schemes proposed by those seeking to classify the various instances of social learning not only irrelevant to their concerns, but also rather impenetrable. However, without such schemes, results of studies of social learning would provide little more than a collection of isolated facts about the development of adaptive patterns of behavior rather than the coherent body of work that has developed over the last few decades. Further, classification has played a critical role in discussion of the extent of overlap of the mental faculties (i.e., cognitive processes) of humans and other animals, an issue that has challenged comparative psychologists since inception of the field.

Over the years, resolving potentially incompatible portrayals of the relationship of animal to human cognition that date back to the origins of modern biology and a dispute between Darwin (1871) and Wallace (1870) as to the continuity of human and animal mind has motivated numerous studies of cognitive processes in animals and led to questions as to whether there exist cognitive processes unique to humankind. Because we will be considering imitation at considerable length later in this chapter, our discussion here focuses on teaching as an example of a behavior, that has emerged from consideration of taxonomies of social learning and, like imitation, was once believed to be uniquely human, but is no longer considered so.

Social Learning and Teaching

Recent reviews by Hoppitt and Laland (2008, 2013), Whiten, Horner, Litchfield, and Marshall-Pescini (2004), and Zentall (2011, 2012) provide extensive discussion of definitions and evidence related to all the principal categories of social learning differentiated in the core literature of the field. The list of categories of social learning is both long and hotly debated. It includes such widely used terms as stimulus enhancement, local enhancement, observational conditioning, response facilitation, emulation, contextual imitation, and production imitation. Space limits to the present chapter, together with the numerous excellent recent reviews of the vocabulary of social learning, have led us to provide here only brief definitions of 14 widely used terms and examples in Table 19.2. We direct interested readers to the reviews cited earlier for more extended analysis and discussion.

We focus instead on the definition and study of teaching, a different and recently topical example of the importance of categorization in organizing the multitude of empirical findings that constitute the foundation of discussions of social learning. To those not familiar with the social learning literature, it may come as a surprise that the reviews cited previously did not include teaching among their categories of social learning. The omission was no oversight. Teaching, although potentially important for social learning, is not generally regarded as a type of social learning as such. Rather, teaching is behavior that a knowledgeable individual performs that facilitates acquisition of some behavior by a naive pupil with whom the teacher interacts. Consequently, a teacher can in principle elicit or encourage any type of learning, whether exclusively social (e.g., imitation) or basically asocial (e.g., trial-and-error learning). For example, a teacher may teach by (a) simply focusing the attention of a potential pupil on some aspect of the environment (local enhancement), (b) exaggerating features of an action for a naive individual to copy (imitation), or (c) encouraging a pupil to persevere

TABLE 19.2

Categories of Social Learning

Category	Examples
Stimulus and local enhancement: Focus of model's behavior on an object or on a location causes learner to adopt a similar focus.	Female quail preferentially associated with males that had been in proximity to other females (Galef & White, 1998); bees focused their foraging on flowers visited more by other bees (Leadbeater & Chittka, 2007).
Observational conditioning: Response of model to a stimulus causes learner to direct a similar behavioral response already in its repertoire to similar stimuli.	Macaque monkeys showed fear responses to stimuli such as snakes after witnessing this in others (Cook et al., 1985).
Contagion/response facilitation: The probability that an individual will engage in a behavior already in its repertoire is increased when it sees another engage in that behavior.	Domestic fowl were more likely to perform preening when others in the flock preened (Hoppitt et al., 2007).
Affordance learning (a form of emulation): A naive individual learns from observing a model behave some operating characteristics (e.g., properties, functions, relationships) of objects or other elements in the environment.	Chimpanzees learned the raking function of a stick-tool from others (Tomasello et al., 1987).
Result and goal emulation: A learner achieves the same result that a model achieved or attempted to achieve but uses a different behavior to do so.	Chimpanzees that witnessed a model pouring water from a bottle into a container to make a peanut float within reach then spat water into their own container to achieve the same result (Tennie et al., 2010); chimpanzees that witnessed failed attempts to open an artificial food object opened the object but in a different way (Call et al., 2005).
Contextual and production imitation: Observing a model behave in a specific way causes an observer to act in the same way. In contextual imitation the observed behavior is already in the observer's repertoire; in production imitation the behavior is novel to the observer.	Pigeons stepped on or pecked a panel according to which of these options they saw a model perform (Zentall et al., 1996). Orangutan trained to "do this" with one set of actions performed full matches to 70% of a battery of 48 other actions, including many judged to be novel (Call, 2001).
Program-level imitation: Learner copies the structural organization of a model's behavior that is novel to the learner, even if component elements are not.	Chimpanzees copied whichever of two novel sequences of the same set of component actions they witnessed (Whiten, 1998); children copied whichever of two novel hierarchical organizations of the same set of component actions they witnessed (Flynn & Whiten, 2008).

Note. Major categories distinguished in the literature on social learning, largely on the basis of analyses by Byrne (2002), Byrne and Russon (1998), Galef (2012), Heyes (1994), Hoppitt and Laland (2008, 2013), Whiten and Ham (1992), Whiten et al. (2004), and Zentall (2012).

in individual trial-and-error learning (Hoppitt et al., 2008). Teaching itself is thus orthogonal to categories of social learning. Teaching has become increasingly important in recent discussions of social learning as a result of growing interest in the relationship between the traditions seen in human and animal populations. Some investigators have suggested that together with imitation, teaching is critical to social transmission of sufficiently precise copies of observed behavior to support the "ratcheting" necessary for the emergence of cumulative culture typical of our own species, and it is either absent (Tomasello, 1990; Galef, 1992) or minimal in other animals (Sanz, Call, & Morgan, 2009; Whiten, 2011).

The scientific study of teaching in animals developed late in the history of comparative psychology, in large part because early definitions of teaching focussed on the intention of a teacher to impart knowledge to a pupil. Some remain convinced of the utility of defining teaching in terms of teachers' intentions (Byrne & Rapaport, 2011). Others disagree (Thornton & McAuliffe, 2012) arguing that identification of instances of teaching and of the behavioral processes supporting such instances should be separated.

Caro and Hauser's (1992) redefinition of teaching provided an operational definition, on the basis of cost–benefit analyses already common in behavioral ecology, which led to a resurgence in the study of teaching in animals and humans. In brief, Caro and Hauser considered teaching to occur when a knowledgeable individual modified its behavior in the presence of a naive individual at a cost (or at least without any immediate benefit) to itself in a way that facilitated the naive individual's acquisition of some behavior.

When defined in this way, many potential instances of teaching were already in the literature. For example, the waggle dance that a successful honeybee forager performs in the hive to alert fellow honeybees to the location of sources of nectar or pollen (von Frisch, 1967), the tid-bitting of gallinaceous birds leading their young to ingest nutritious foods (Sherry, 1977) or the mobbing and alarm-vocalizations that help naive individuals learn to recognize potential predators (Curio, 1988) all satisfy Caro and Hauser's (1992) criteria. Several interesting cases of teaching in animals meeting Caro and Hauser's criteria have been recently identified, perhaps most compelling among them is the adult provisioning of dangerous prey to young meerkats (*Suricata suricata*).

Learning to handle toxic prey: Meerkats. Young meerkats are largely dependent on provisioning by adults until 2 to 3 months old, when they begin to forage independently for insect prey, including potentially dangerous scorpions (Thornton & McAuliffe, 2006). Adult meerkats usually immediately consume prey they capture. However, in the presence of young meerkats, adult meerkats will often kill or disable, rather than eat, captured scorpions (in the latter case, removing the scorpions' stingers) so as to bring intact scorpions to juveniles.

Most spectacularly, adult meerkats modify their provisioning behavior in response to the perceived age of the young they are provisioning, increasing the frequency of bringing intact scorpions as the young mature and become increasingly competent to handle such dangerous prey. Playing recordings of begging calls of an older pup to an adult providing scorpions to a young pup causes the adult to increase the frequency with which it presents intact scorpions, even though the recipient is not yet ready to handle them. Conversely, playing the calls of young pups to adults provisioning older juveniles increases the frequency with which adults deliver disabled or killed scorpions that would normally be given to younger pups.

Further, as Caro and Hauser's (1992) definition of teaching requires, not only did provisioning adults incur a cost, providing prey to young they could have eaten themselves, but they also facilitate the development of prey-handling skills in the juveniles they provisioned. Young meerkats provided with disabled scorpions learned to handle intact scorpions more rapidly than pups artificially provisioned with either dead scorpions or a hard-boiled egg.

Learning the way to food and nest site: Tandem running in ants. Equally compelling evidence of teaching is available in *Temenothorax albipeenis,* a species of ant in which a successful forager that knows the location of a food source travels in an unusual way toward the food in tandem with a naive nest mate, pausing while the follower looks around, apparently examining landmarks along the route, and moving rapidly toward food only after its follower taps it with its antennae. As a consequence of this unusual behavior, the leader ant delays its return to food, taking four times longer to travel in tandem with a naive ant than it would if traveling the same path alone, whereas naive followers find food faster when following a knowledgeable leader than when searching for food on their own. Also, after following, naive ants return more directly to the nest site they share with their leader ant than the leader ant did after it first discovered the food (Franks & Richardson, 2006).

Teaching in chimpanzees and humans. Given the discovery in ants, bees, and various bird and mammal species of behaviors that met Caro and Hauser's (1992) criteria for teaching, it came as something of a surprise that many years of observation of chimpanzees in natural habitat provided essentially no evidence of teaching in this closest extant relative of humans (*Homo sapiens*), the planet's most accomplished teachers. (For an alternative view of teaching in chimpanzees, see Boesch, 2012.) Indeed, absence of evidence of teaching in chimpanzees led some to question the prevalence of teaching in preliterate human societies (Laland & Hoppitt, 2003).

The older ethnographic literature, in which formal verbal instruction of the sort common in the Western world served as the model of teaching, provided few reports of such instruction. However, more recent anthropological investigations relying on a definition of teaching consistent with Caro and Hauser's (1992) have provided compelling evidence that teaching is present in indigenous societies (for examples see Hewlett, Fouts, Boyette, & Hewlett, 2011; Kline, Boyd, & Henrich, 2013). The importance of teaching relative to other forms of learning (e.g., imitation, trial and error) in skill development in preliterate societies remains an open question.

The peculiar phylogenetic distribution of known instances of teaching in insects, gallinaceous birds, and humans, but not chimpanzees, raises important questions as to whether teaching is a single process or many different processes. As Premack (2007) indicated, animal teachers differ profoundly from their human counterparts in that the former always have a single domain in which they teach, whereas human teaching is a "domain-general competence" (p. 13862), with teachers facilitating acquisition of innumerable skills. Clearly, in discussing teaching as Caro and Hauser (1992) defined it, we are dealing with analogy not homology. The function of teaching is common across instances, the mechanism is surely not.

Constructing taxonomies of social learning requires attention to similarities in the behaviors of members of species that are only distantly related to one another, an approach to the analysis of behavior that some find hard to justify. If such an approach to behavioral comparison were all that the field of social learning had to offer, criticism of its contribution might well be valid. However, as our discussion will show, in harmony with the phylogenetically based comparative psychology that Romanes (1884), Lorenz (1950) and others advocated, comparative studies of social learning have involved investigations of similarities and differences in social learning in closely as well as distantly related species.

COMPARISONS OF CLOSELY RELATED SPECIES

Comparison of behavioral phenotypes of closely related species might be assumed to lie at the heart of any discipline calling itself comparative psychology. However, in attempting to review the relevant literature, we have found such comparisons remarkably rare, with the exception of comparisons between our own species and those with which we share our most recent common ancestry, the great apes, especially the most frequently studied of our closest primate relatives, the chimpanzee. Table 19.3 lists 25 articles comparing the behavior of humans with that of other apes. By contrast, our explorations of the literature revealed few comparative studies of social learning in two or more closely related nonprimate species.

Rationales for a Comparative Psychology of Social Learning

The rationales that authors offer for pursuing comparisons between closely related species vary in

TABLE 19.3

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Direct comparisons				
Nagell et al., 1993	24 × 2 yr	15 chimps × 4 yr–8 yr	human models—flip over rake tool to more efficiently rake in reward, versus tool already flipped	Chimpanzees were no more likely to flip tool to its more efficient form having observed this modeled than having seen use of a tool already flipped. By contrast, children were more likely to flip tool in the observation condition.
Tomasello et al., 1993	16 × 1.5 yr–2.5 yr	6 chimps & bonobos × 3 yr–21 yr	human models—battery of 24 modeled actions incorporating specific, unusual acts on objects and their outcomes	Three human-enculturated apes showed levels of imitation (copying both actions and outcomes) similar to those of children tested. By contrast, three mother-reared apes were rarely judged to imitate.
Call and Tomasello, 1995	24 × 3 yr–4 yr	14 orangs × “juvenile and adult”	human + conspecific models—different sequences of pull, push, and rotate handle to release food; how sequence worked was opaque	Orangutans showed no evidence of learning the particular acts (e.g., rotate vs. pull) or sequences (e.g., rotate then push) they had witnessed, whether the model was a human or orangutan. By contrast, 37% of three-year-old children and 69% of four-year-olds matched sequence witnessed.
Carpenter and Tomasello, 1995	6 × 18 mos	6 chimps × 3 yr–21 yr	analyzed the joint attentional behavior of subjects	Amongst the apes, the extent of joint attentional behavior was positively correlated with imitative performance; enculturated apes were more like children in attentional behaviors.
Whiten et al., 1996	7 × 4 yr–8 yr	8 chimps × 4 yr–5 yr	human models—alternative actions on three components of artificial fruit, to extract rewards	Both chimpanzees and children matched the model’s actions applied to one component whereas children matched for two components.
Call et al., 2005	48 × 2.5 yr	50 chimps × 4 yr–40 yr	conspecific models—for two alternative ways to open a tube, subjects saw (attempted) actions only, results only, both, or neither	Chimpanzees mainly reproduced only the results of alternative actions and tended to avoid the attempted but failed approach witnessed, whereas children often matched the latter.
Horner and Whiten, 2005; McGuigan et al., 2007, 2011	16 × 3 yr–5 yr	12 chimps 4 yr–6 yr	human models—causally relevant versus causally irrelevant actions; visibly so versus opaque	Chimpanzees tended to match sequence and type of actions in opaque condition but omit causally irrelevant actions in transparent condition. Children copied irrelevant actions in both conditions.
Tennie et al., 2006	201 × 1 yr–2 yr	14 chimps, 6 gorillas, 8 orangs × <5 yr and >15 yr	conspecific models—for two alternative ways to open a small door, subjects saw full action, only (“ghost”) door movement, or no model	Apes did not match the alternative they witnessed in either condition (however, they succeeded in 7/8 of no-model condition, so had little need to learn by observation). By contrast, 1.5- to 2-year-old children tended to copy in both full model and ghost conditions.
Horner et al., 2006	31 × 3 yr–4 yr	22 chimps × 11 yr–42 yr	conspecific models—tool used to extract reward from two-action artificial fruit	Alternative methods of opening were faithfully transmitted along chains of 5 and 6 chimpanzees, and both chains of 8 children.

(*continues*)

TABLE 19.3 (*Continued*)

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Herrmann et al., 2007	105 × 2.5 yr	106 chimps × 3 yr–21 yr; 32 orangs × 3 yr–10 yr	human models—solutions to three problems chimpanzees did not display in baseline tests were modeled once (e.g., bang tube on ground to release reward inside)	Chimpanzees and orangutans never matched, whereas children always did. This was the most marked of all species differences in 6 tests of communication, theory of mind, and physical understanding.
Horner and Whiten, 2007	12 × 3 yr–4 yr	9 chimps × 2 yr–6 yr	human models—correct insertion of stick-tool to extract reward from tube with trap in it, versus initially incorrect move followed by correct approach, and a stimulus enhancement condition	Neither chimpanzees nor 3- to 4-year-old children benefited from viewing errors as well as correct and successful approaches. None gained an understanding of the nature of the trap problem. 5- to 6-year-old children were more successful but relied little on copying model behavior.
Hopper et al., 2008	40 × 3 yr–5 yr	32 chimps × 11 yr–44 yr	conspecific models—subjects saw door moved left or right by model, or only “ghost” door movement, or same with passive conspecific present, or no model	Chimpanzees matched the door direction witnessed only on first trial in the ghost condition (thus emulating) but did so consistently if viewing a conspecific perform the action. Children were the same except were also more likely to copy door movement when a passive conspecific was present.
Buttelmann et al., 2008	24–28 × 14 mos in each of 3 studies	16 chimps, 5 gorillas, 5 bonobos, 7 orangs, 3 yr–31 yr	human models—in three variations, subjects saw model use tool to obtain reward when unnecessary or when necessary because access blocked	In all three studies, infants were more likely to copy use of the tool when it was freely used rather than necessary, whereas apes did not, with the exception of the orangutans (cf. Buttelmann et al., 2007).
Tennie et al., 2009	27 × 4 yr	7 chimps, 6 gorillas, 8 orangs, 5 bonobos (no ages)	human models—either make a loop of wool and use it to lasso a peg on a board and pull it close to gain reward, or show the board movement only	No ape made a loop in any condition. One child made and used a loop after the object movement demonstration but 9/12 did so after seeing the act modeled.
Haun et al., 2012	16 × 2 yr–2.5 yr	15 chimps × 6-21 yr; 12 orangs × 6 yr–12 yr	Three conspecific models—placed tokens in one of three containers, versus one model posting in alternative container	Chimpanzees and children tended to match the majority choice, but orangutans did not.
Dean et al., 2012	35 × 3 yr–4 yr	74 juvenile and adult chimps, 22 capuchins	conspecific models—three-stage puzzle box permitting cumulative learning of solutions to obtain increasing rewards	Only children attained Level 3 in substantial numbers, evidencing superior imitative matching, teaching, sharing, and cooperation.
van Leeuwen et al., 2014	23 × 3 yr–4.6 yr	14 chimps × 7 yr–36 yr	conspecific models—participants received conflicting personal and social information on reward locations	Both children and chimpanzees favored personal to social information but when no personal information was available, children used social information whereas chimpanzees did not.
Haun et al., 2014	18 × 24 mos–33 mos	12 chimps × 6 yr–21 yr; 12 orangs × 5 yr–12 yr	conspecific models—individuals learned a reward location preference, then witnessed three conspecifics preferring another	Just over half the children switched to conform to the majority but only one chimpanzee did so and no orangutans did.
Vale et al., 2014	36 × 5 yr	32 chimps × 15 yr–44 yr	conspecific models—video of harvesting from resource rich (12 sec interval) or poor (84 sec) boxes colored differently	The two species displayed almost exactly the same tendencies to prefer (by approximately 2:1) the resource rich option.

TABLE 19.3 (*Continued*)

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Claidiere et al., 2015	97 × 5 yr–7 yr	16 chimp adults; 14 adult + juv capuchins	conspecific models—individuals not acting prosocially, by choosing one of two options that would reward a conspecific, experienced prosocial responses	An increased propensity to choose a prosocial option was recorded in chimpanzees and older children (7 yrs) but not in capuchins and younger children (5 yrs).
Ape experiments with earlier (or later) child studies specifically compared to them				
Call and Tomasello, 1994	Nagell et al., 1993	16 orangs × 6 yrs–34 yrs	human and conspecific models—replication of Nagell et al. (1993) with orangutans	Like the chimpanzees in the Nagell et al. study, orangutans were no more likely to flip tool to its more efficient form having observed this modeled than having seen use of a tool already flipped.
Whiten et al., 2005	Flynn and Whiten, 2012; Hopper et al., 2010; Whiten and Flynn, 2010	3 groups of chimps, total = 40 × 6 yr–40 yr	conspecific models—two alternative ways modeled, using same tool to release food (plus no model control)	Unlike controls, 15/16 chimpanzees in each experimental group mastered task and adopted whichever of the two forms of tool use was seeded by the model in their group. Children also showed spread of the seeded alternatives, but more exploration of alternatives, so overall lower fidelity.
Tomasello and Carpenter, 2005	Bellagamba and Tomasello, 1999; Carpenter et al., 1998	3 chimps × 5 mo–4 yr	human models in all four studies—instrumental versus arbitrary acts; failed attempts; accidental versus intended acts; style of action done	One chimpanzee copied both arbitrary and instrumental acts; others copied or attempted to copy only the instrumental acts. All three chimpanzees showed evidence of completing intended but not achieved outcomes; did not mimic failed action attempt itself. Chimpanzees copied intentional more than accidental acts, similar to 16-month-old children (Carpenter et al., 1998). Unlike some 12-month-old human infants, chimpanzees copied outcomes but rarely matched style of action used.
Marshall-Pescini and Whiten, 2008	Whiten et al., 2009	11 chimps × 2–6 yr	human model—first shown use tool to extract honey, versus no model condition; then shown more complex use of tool to unlock top and gain greater reward	Chimpanzees learned the first fishing technique by observation but then did not learn the second, more complex approach. A majority of children did show cumulative learning of the second method.
Buttelmann et al., 2008	Gergely et al., 2002	8 chimps × 3 yr–8 yr	human model—touch panel to switch on light or sound using head, foot, or bottom, with hands occupied versus not occupied	Like human infants, enculturated chimpanzees were more likely to copy actions performed with the hands free, indicating a corresponding grasp of rationality in the actions of others.

detail, but at their core is the pursuit of evolutionary explanations for differences and similarities. Assuming that differences in social learning are manifest even when any two species being compared are exposed to similar rearing environments, then the root of any differences is attributable ultimately to genetic factors, which in turn are a result of selection by different ancestral ecological niches of the species compared. For example, Coolen, van Bergen, Day, and Laland (2003) showed that nine-spined sticklebacks (*Pungitius pungitius*) used the foraging behavior of other fish to identify the higher quality of two foraging patches, whereas closely related three-spined sticklebacks (*Gasterosteus* *aculeatus*) did not. The authors noted that the latter species has morphological features that protect against predatory attack that the former does not and that predatory fish preferentially target the relatively unprotected nine-spined species. Accordingly, nine-spined sticklebacks in Coolen et al.'s experiments tended to retire among protective vegetation and observe other fishes' foraging success, then later used those observations to decide whether to forage, whereas the more robust three-spined individuals would rapidly approach fish seen feeding, and were therefore less likely to learn by observation which feeding site was the more productive. The authors thus directly related differences in social learning to differences in predator-related habitat choices.

Because behavioral adaptations typically take the form of a complex of different components, their adaptive significance may not be related directly to habitat preferences, but to other central aspects of a species' adaptive behavioral profile. Thus, for example, Lefebvre, Palameta, and Hatch (1996) compared the propensity for social learning in the food finding behavior of a gregarious columbid (*Columba livia*) with that of a more solitary columbid (*Zenaida aurita)* to test the hypothesis that social learning might represent an adaptation to group living.

A similar hypothesis motivated a comparative study focused on mate-choice copying, in which individuals prefer to try to mate with partners they have witnessed others have already chosen. King, von Ende, and Moran (2013) predicted mate-choice copying would be stronger in a species of fish exhibiting parental care than one that simply hides its eggs, because it would be costlier for the former to make a bad mating choice. In fact, neither the study by King et al. nor Lefebvre et al. (1996) obtained data supporting the hypotheses tested. Nevertheless, both illustrate clearly a common rationale for conducting comparative studies.

Range and Virányi's (2013, 2014) comparisons of social learning in wolves and dogs illustrate a similar principle, although in dogs the "ecological niche" to which adaptations are predicted to have occurred is the cluster of features that characterise human domestication. In their first paper, the authors found that when the social learning tested was simple local enhancement (learning which alternative location was the more productive foraging site), the two species showed similar social learning, whether from conspecifics or human models. However, in the later paper, when dogs and wolves were compared on the possibly higher-level process of imitation (matching whether a paw or mouth was used to press a lever), wolf cubs were more attentive to conspecific models than were dogs, and only the wolves evidenced significant imitative learning. The authors suggested that the latter result reflects an adaptation for attending closely to actions of others necessary for the cooperativeness so important to wolf-pack life.

Examining the 100+ papers that cited the comparative studies reviewed previously, as well as the 1600+ articles on social learning cited in the recent monograph of Hoppitt and Laland (2013) suggested these rather meagre pickings exhausted the comparison of closely related, nonprimate species. In contrast, studies in which humans (typically children) are compared with other great apes (most often chimpanzees) have become numerous through the last 2 decades (Table 19.3).

Anthropocentric search for uniquely human characteristics has motivated many studies comparing children and chimpanzees. Possible similarities (allowing inferences about the phylogenetic history of social learning and culture from which present day humans' psychological capacities evolved) and possible differences (which may help to explain the yawning gap between us and "them" resulting in a human propensity for cumulative culture that has allowed us to dominate the planet; Whiten, 2011) are of interest. Still, fundamentally the rationale for comparisons among primates, like that for comparisons among nonprimates is to define similarities and differences and to explain them in evolutionary terms, elucidating their adaptive fit to the ecological niches humans and apes occupy. Apes live in tropical forests, whereas early human ancestors moved first into savannahs and ultimately far beyond. However, as noted earlier, social learning phenomena are likely to be adapted not only to physical environments, but also to other behavioral and psychological features, which in the case of humans includes hyper-cooperation (see Volume 1, Chapter 13, this handbook and Chapter 20, this volume), theory of mind (see Chapter 32, this volume), and other sophisticated sociocognitive features (Whiten & Erdal, 2012).

Methods and Pitfalls

A basic but powerful method of testing experimentally for social learning, exemplified in many nonprimate and primate comparative studies, is the *two-action method*. In such studies, observer animals are exposed to models performing either of two different actions directed toward the same object and the observers' tendency to perform the option they witnessed is evaluated. Ideally, a control group is included in which no model of any kind is available. Contrasts in task success between the two model conditions and the no-model control condition permit conclusions about the existence of some kind of social learning, whereas contrasts between the two different model conditions provide evidence about what is learned. For example, if the two different options available to subjects during testing involve simply feeding at one location rather than another, the conclusions drawn will concern the operation of local enhancement; if the two options are different acts (like moving a lever with paw versus mouth), the conclusions reached may concern imitation. However, several ape studies go beyond these simple contrasts in various ways outlined in Table 19.3 and are discussed in further detail following.

For example, in some studies the two-action approach has been extended to examine the potential for cultural transmission of initially seeded options, either along *transmission chains* of individuals in which each participant becomes a model for the next, or in *open diffusion* designs where an individual is removed from its group, trained, then returned and the question becomes whether the seeded behavior will spread (Whiten & Mesoudi, 2008). Alternatively, *ghost conditions*, in which the outcomes normally produced by a model's actions are made to happen without involvement of a model (e.g., Hopper, 2010), have been applied comparatively to determine whether observation of movement of an apparatus is sufficient for learning, or social learning occurs only when an agent is observed moving a portion of the environment.

Human–ape comparative studies have not only been particularly productive (Table 19.3) but also serve to illustrate several important problems in achieving effective comparisons. Ideally, to make valid interspecies comparisons in social learning, all variables other than species must be held constant. Assuring such equivalence is particularly problematic in the case of humans and chimpanzees. Because of the requirements for experimental control in studies of social learning, only a handful of experiments have been completed with primates living in their natural environments, and these studies have concerned lemurs and monkeys (e.g., Gunhold, Whiten, & Bugnyar, 2014; Schnoell, Dittmann, & Fichtel, 2014; van de Waal, Claidière, & Whiten, 2015) rather than apes. Relevant field experiments have begun with apes, but have yet to incorporate models and controls to rigorously test for social learning as have other primate studies (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011; Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009). Indeed, all studies listed in Table 19.3 have been conducted with captive apes typically housed in primate research centers.

The communities that captive chimpanzees live in are typically small compared to those of wild chimpanzees and captive environments, regardless of "enrichment," are impoverished compared with the wild or compared with the environments of human children with which captive chimpanzees are typically compared. Thus, species differences are confounded with environmental complexity.

Experimental tests lead to further difficulties in comparing like with like. In approximately half the cases in Table 19.3, the model for both species has been a human: A conspecific for children but an alien species for apes. Apes may find the shape and manipulative configuration of the hand of the model less easily identified with than children. Such difficulties may put chimpanzees at a disadvantage in revealing their true behavioral capacities, so failure of chimpanzees to express some capacity seen in children must be treated with caution. However, outcomes in which either apes or children exhibit a capacity the other species does not are at the very heart of a comparative approach that aspires to identify similarities and differences between species. Such difficulties in achieving valid comparisons have been recognized since the early days of comparative psychology, but are particularly significant in the case of human and nonhuman primates.

Humans and Other Apes Compared

Despite the hurdles to research discussed previously, over the last 2 decades, comparative studies have produced a rich literature comparing social learning in humans (typically children) and nonhuman great apes. A selection of the studies listed in Table 19.3 are discussed as providing evidence relevant to a series of significant questions.

Imitation versus emulation. Perhaps no issue has pervaded the human–ape social-learning literature more than that of the role of imitation and emulation. The discussion began when, in a study of chimpanzees' social learning of using a rake to acquire food, Tomasello, Davis-Dasilva, Camak, and Bard (1987) observed that, although most chimpanzees did not copy the particular motor act a model used to acquire food, they did apply the tool more successfully than could be accounted for by mere stimulus enhancement. The authors suggested that the chimpanzees observed "the relation between the tool and the goal" (p. 182) and learned "to use the tool in its function as a tool" (p. 182), a type of social learning that Tomasello (1990) later labeled *emulation*, noting that unlike the case of imitation, in emulation the observer may act "in any way it may devise" (p. 284) to achieve the goal it had seen attained.

A series of experiments comparing children's social learning with that of chimpanzees and focused on emulation followed. In the first, children copied a human model's trick of flipping over a pronged rake to pull in a reward and were described as imitating, unlike chimpanzees using the tool without replicating the flip action and therefore described as emulating (Nagell, Olguin, & Tomasello, 1993). Call and Tomasello (1994) found similar copying in orangutans (*Pongo pygmaeus*).

Using an ingenious and quite different approach, Call and Tomasello (1995) allowed orangutans to watch human and conspecific models operating a lever to release food from an opaque box which obscured the goals of the action, thus precluding emulation and leaving imitation of the demonstrator's action with the lever as the only method for observers to succeed. Various alternative actions like pulling, pushing or rotating the lever, and particular sequences of these were effective in releasing food. Young children had some success in copying such actions, but consistent with the hypothesis that orangutans are limited to emulation and cannot imitate, they failed miserably in the task.

However, this dichotomy between imitation and emulation subsequently proved an over-simplification. Sue Savage-Rumbaugh indicated that chimpanzees and bonobos (*Pan paniscus*) participating in her language learning studies appeared quite capable of imitation and a suite of formal tests soon confirmed her observations (Tomasello, Savage-Rumbaugh, & Kruger, 1993). However, imitation was seen only in chimpanzees that, like those in Savage-Rumbaugh's studies, had rich daily interactions with humans, not in other, mother-reared chimpanzees. The difference in capacity of these enculturated and mother-reared chimpanzees led to the hypothesis that enculturation could shape apes' attention to humans sufficiently to reveal human-like capacities for imitation.

Studies other than the comparative ones reviewed in Table 19.3 also demonstrate imitative responses in apes. Such studies in single species include "Do-as-I-do" experiments in which chimpanzees and orangutans were trained to match a series of actions and were then tested with a battery of more novel gestures and bodily actions (Call, 2001; Custance, Whiten, & Bard, 1995).

Other direct comparative studies took different approaches. Horner and Whiten (2005), for example, hypothesised that some degree of imitation and emulation might be present in the repertoires of children and apes (even if to a different extent), but are expressed differentially according to context. Horner and Whiten presented young children and wild-born chimpanzees with a model who used a series of tool-based manipulations to extract food from either an opaque or a transparent artificial fruit, in both cases incorporating some actions that were not causally necessary to complete the task (see Chapter 27, this volume). In the case of the transparent apparatus only, an observer could see that there was no connection between these extraneous acts and extracting the reward. It was anticipated that an intelligent imitator would imitate the whole series of actions observed to result in success in the case of the opaque apparatus that prevented determination of which actions were unnecessary, whereas those faced with the transparent version of the apparatus would omit unnecessary actions, taking a more emulative approach. The expected result was observed in chimpanzees, leading to the conclusion that chimpanzees possess a “portfolio” of alternative social learning capacities that includes imitation and emulation (as well as local enhancement) that may be expressed differentially according to circumstances (Whiten, Horner, & Marshall-Pescini, 2005). Surprisingly, and unlike chimpanzees, children did not act like the “intelligent imitator” sketched previously; instead children tended to imitate entire sequences including any causally unnecessary elements, even when working with the transparent artificial fruit that made the extraneous nature of some actions apparent.

Overimitation. Developmental psychologists quickly became fascinated with the discovery that children copied clearly irrelevant actions, labeling the phenomenon *overimitation* (Lyons, Young, & Keil, 2007). Further research has not only replicated the finding of overimitation in several cultures (Nielsen & Tomaselli, 2010; Nielsen, Mushin, Tomaselli, & Whiten, 2014), suggesting that overimitation may be a human universal, but also has led to the surprising conclusion that the tendency to copy even apparently causally irrelevant acts becomes stronger throughout childhood and into adulthood (McGuigan, Makinson, & Whiten, 2011; McGuigan, Whiten, Flynn, & Horner, 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009).

Given that chimpanzees in the Horner and Whiten (2005) study could discriminate necessary from useless acts, whereas children copied both, a picture emerges of greater copying fidelity in humans than in apes and an ability to imitate in both primate species. Overimitation, by its very nature, suggests that our own species is prepared to copy what an intentionally acting model does, even when her acts appear bizarre. Chimpanzees, although more ready than children to emulate when a model behaves bizarrely, may nevertheless copy quite elaborate sequences when the relevant causal structure of the task is opaque. It is important to note, however, that although we now have a large corpus of overimitation studies in children, data on chimpanzees rests on only a single study (Horner & Whiten, 2005).

Why overimitation occurs in humans has become a subject of much debate and investigation. Possibly, we are such a thoroughly cultural species that it is simply a good rule of thumb to treat adults’ intentional actions as generally worth copying, even when the relevance of aspects of those actions is mysterious, which is often the case given the opacity and complexity of the technologies about which children need to learn (Lyons et al., 2007; Whiten et al., 2005). Alternatively, overimitation may serve social functions, identifying and building relationships with others (Nielsen, Simcock, & Jenkins, 2008). Other explanations for overimitation have been proposed, but this is not the place to review this burgeoning literature; the reader is referred to Kenward (2012) for a review and further hypotheses.

Rational imitation. The concept of rational imitation originated in a replication by Gergely, Bekkering, and Király (2002) of an earlier study by Meltzoff (1988) that had shown young infants imitating the actions of an adult who used h[illegible]ead rather than her hands to contact a box and make it light up. The clever twist in Gergely et al.’s (2002) experiment was to add a condition in which the adult had a blanket round her arms, so only her head was free to contact the box. Infants were much less ready to imitate in this situation.

Gergely et al. (2002) concluded that infant imitation is guided by a sophisticated theory of action that discriminates a freely chosen act worth copying from an action constrained in some way and therefore to be ignored. Buttelmann, Carpenter, Call, and Tomasello (2008) completed a study with chimpanzees aiming to replicate and extend Gergely et al.’s (2002) study. Like the human infants, these human-reared enculturated chimpanzees, were more likely to imitate head-bobbing by a model with free hands, than by a model whose hands were occupied (e.g., holding a box).

Such context sensitivity in copying in chimpanzees is consistent with their lack of susceptibility to overimitation as context sensitivity and a failure to imitate irrelevant actions can be considered "rational" discriminations. In human children, however, the existence of rational imitation and overimitation presents a puzzle in need of resolution (Whiten, 2013). Perhaps the discovery that overimitation continues into adolescence (Nielsen & Tomaselli, 2010) and even into adulthood (McGuigan et al., 2011) provides evidence that overimitation is not so irrational after all, but most of the time serves members of our species well, on different occasions promoting acquisition of complex cultural skills, supporting social integration, facilitating social conventions, and various combinations of these.

Preferential copying of intentional acts. As part of a battery of experiments on the social learning capacities of three juvenile enculturated chimpanzees, Tomasello and Carpenter (2005) sought to replicate their earlier study (Carpenter, Akhtar, & Tomasello, 1998) showing that young children discriminated and preferentially copied intentional actions rather than equivalent actions engineered to appear accidental. Discrimination of intentional acts was also found in chimpanzees, so selectivity in chimpanzee imitation extends to the intentional/accidental distinction and that of rational choice previously discussed.

Moreover, in a related experiment, Tomasello and Carpenter (2005) found that, like human infants studied by Meltzoff (1995), young chimpanzees who witnessed a human model attempting, but failing, to complete an action (e.g., placing a loop over a stand), would successfully complete the action, rather than mimic the observed (failed) performance, thus achieving an appropriate outcome they had never witnessed. In both sets of experiments (accidental versus intentional, and failed attempts) young humans and young chimpanzees displayed an approach to imitation that was sensitive to the intent of the performer of an observed action (see Chapter 32, this volume).

Cultural transmission and diffusion. Some things that may be learned socially (e.g., which bush is fruiting today) have a limited window of existence, whereas other socially acquired information may be sustained and transmitted repeatedly, diffusing through a group or even across generations to become a tradition. Over the last half century, evidence for such cultural traditions has progressively accumulated from long-term field studies of primates.

Researchers studying chimpanzees and orangutans at multiple field sites have collaborated to identify scores of behaviors of different kinds (e.g., tool use, foraging, sexual and social habits) present at some sites but not at others and to exclude, insofar as possible, any ecological or genetic explanations for regional differences in behaviors (Krützen, Willems, & van Schaik, 2011; van Schaik et al., 2003; Whiten et al., 1999). Although such ape traditions are relatively insignificant in comparison with the vast cultural achievements of humans, field studies suggest that humans share with the apes an unusual degree of cultural complexity (Whiten, 2005, 2011).

To date, observational studies of ape traditions lack validation from experimental interventions carried out in the wild, an enterprise that, because of its logistic difficulties remains in its infancy in primatology (e.g., Gunhold et al., 2014; van de Waal, Borgeaud, & Whiten, 2013). However, several cultural diffusion experiments carried out with captive primates, some directly comparing the performance of children with that of other apes are now available. In the first such study, Horner, Whiten, Flynn, and de Waal (2006) established transmission chains in which a first individual was trained to open an artificial fruit using one of two techniques (sliding a hatch versus lifting a small door), then acted as the model for a second individual who became the model for a third, and so on for so long as each individual was successful (whichever method they used). Such chimpanzee chains were limited by participant availability. Nevertheless, chains of 5 or 6 individuals were achieved in which seeded alternatives were transmitted faithfully, thus simulating multiple-generation transmission. Children exposed to the same conditions faithfully transmitted alternatives along chains of 10 individuals. Transmission fidelity was sufficient in both species for multiple-generation transmission of distinct, if minimal, incipient traditions.

An alternative diffusion experiment with chimpanzees described as involving an open diffusion (Whiten et al., 2005) was subsequently matched with a child study using exactly the same apparatus (Flynn & Whiten, 2012; Whiten & Flynn, 2010). In all three studies, models were first trained to use a tool to either lift or poke a blockage to extract rewards from an apparatus. Each model was then reunited with its group (nursery groups in the case of children). In both species, different incipient traditions were established. Cultural corruption first appeared in the groups of children, with the difference between groups disappearing on the second day of the study. Children then copied the "corrupt" variants.

Fading of the initially established group differences in children was largely because of their greater tendency to explore and use the tool in as many ways as possible. Thus, the greater fidelity of transmission often claimed for humans, as compared with chimpanzees, was not evident in this study, which presently is the only direct comparison of children and apes of social transmission in an open diffusion experiment. The message, however, is not that humans are less capable of faithful copying, but rather the outcome of such experiments will depend on the fit between the challenges of the task and the intellects of the participants. In the present case, children were more likely to explore the affordances of the task, and their behavior highlights the difficulty of comparing like with like in comparative psychological studies of social learning.

Cumulative cultural evolution. It is frequently asserted that cumulative cultural evolution fundamentally separates our species from all others (see Volume 1, Chapter 15, this handbook and Chapter 20, this volume). However, experimental investigations of cumulative culture are rare. Marshall-Pescini and Whiten (2008) explored cumulative culture in chimpanzees, later applying the same experimental design to young children (Whiten et al., 2009). Participants in these studies first learned by observation a relatively simple method to extract honey from a foraging device (opening a small hatch with one hand while using the other hand to insert a probe to remove a small amount of honey). A familiar human caretaker then modeled a more complex procedure that incorporated and built on the first method in cumulative fashion (inserting the probe into an obscured hole to allow the whole top of the device to hinge open so all the honey and nuts inside became available).

Chimpanzees assigned to a group whose members had not learned the dipping technique discovered the more complex technique for themselves, yet surprisingly, none of those who had learned to dip shifted to the more complex, more productive second technique. By contrast, most children did shift to the more productive technique. The authors concluded that chimpanzees failed to evidence cumulative cultural learning because of a remarkable conservatism leading them to become "stuck" on the first, satisficing technique they learned (see Chapter 28, this volume). Subsequent studies have also highlighted such behavioral conservatism in the context of social learning in chimpanzees (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2008).

Dean, Kendal, Schapiro, Thierry, and Laland (2012) took a different approach, presenting to capuchin (*Sapajus apella*), chimpanzees and children a device that offered increasing rewards attainable in successive steps: Children were far more successful than primates at attaining the higher levels. The nonhuman groups, even when provided with conspecific models trained to attain the highest level, failed to advance beyond the first level where they received lesser rewards and provided further evidence of the conservative disposition found by Marshall-Pescini and Whiten (2008). Dean et al. (2012) pointed to children's tendency to copy witnessed acts, to overtly teach one another, and to share rewards as supporting children's cumulative progress (see Chapter 20, this volume).

Just what holds chimpanzees and other primates back remains mysterious, but work on the issue continues. For example, Vale, Flynn, Lambeth, Schapiro, and Kendal (2014) showed that chimpanzees, like children, recognize when others are gaining rewards superior to their own, so an inability to compare one's own success with that of others appears not to be a limiting factor (see Volume 1, Chapter 44, this handbook and Chapter 16, this volume). Others have shown some capacities in apes for cumulative learning (Lehner, Burkart, & van Schaik, 2011; Manrique, Völter, & Call, 2013; Yamamoto, Humle, & Tanaka, 2013), but only the last of these involved social learning and even there the evidence remains relatively qualitative.

Conclusion. The research outlined previously and in Table 19.2 has established a range of features of social learning shared by humans, other apes, and by inference our common ancestors. These features include a portfolio of context-sensitive social-learning processes including emulation and imitation that offer sufficient copying fidelity for the transmission of tool use and other behaviors within groups. Studies comparing social learning in children and apes have also sharpened our understanding of species differences in a capacity or motivation for high-fidelity copying, resulting at its extreme, in overimitation (see Volume 1, Chapter 20, this handbook). Possibly, such differences, along with other characteristics such as hyper-cooperativeness and sharing, support human's special propensity for cumulative culture.

CONCLUSION

In the 19th century, when Romanes first proposed guidelines for a successful comparative psychology, he could never have imagined the diversity and richness of the field that was to develop from his pioneering work. Although study of animal social learning is a relative newcomer to the effort to understand the behavioral capacities of animals, in the last 40 years, the literature concerning animal social learning has grown at an astonishing rate and now makes a substantial contribution to our attempts to address the issues Romanes first raised.

The wealth of materials now available has required that any review of the comparative psychology of social learning be selective. Here, we have striven to provide readers with a first appreciation of the range and scope of this ever-expanding field. Those seeking greater engagement with the area should refer to the reviews listed in Appendix 19.1.

APPENDIX 19.1 RECENT REVIEWS OF SOCIAL LEARNING

Galef, B. G., Jr. (2012a). Social learning in rats: Historical context and experimental findings. In T. Zentall & E. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (2nd ed., pp. 803–818). Oxford, England: Oxford University Press.

Galef, B. G., Jr. (2012b). Social learning, tradition, and culture: Data and debate. In K. Yasakawa & Z.-T. Martinez (Eds.), *Animal behavior: How and why animals do the things they do* (Vol. 1, pp. 115–150). Santa Barbara, CA: Praeger.

Garriepy, J.-F., Watson, K. K., Du, E., Xie, D. L., Erb, J., Amasino, D., & Platt, M. L. (2014). Social learning in humans and other animals. *Frontiers in Neuroscience*, *8*, 58. http://dx.doi.org/10.3389/fnins.2014.00058

Hopper, L. M., & Whiten, A. (2012). The comparative and evolutionary psychology of social learning and culture. In J. Vonk & T. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 451–473). Oxford, England: Oxford University Press.

Kendal, R. L., Galef, B. G., Jr., & van Schaik, C. P. (2010). Social learning research outside the laboratory: How and why? *Learning and Behavior*, *38*, 187–194. http://dx.doi.org/10.3758/LB.38.3.187

Laland, K. N., & Galef, B. G., Jr. (Eds.). *The question of animal culture*. Cambridge, MA: Harvard University Press.

Nielsen, M., Subiaul, F., Galef, B. G., Jr., Zentall, T. R., & Whiten, A. (2012). Social learning in humans and nonhuman animals: Theoretical and empirical dissections. *Journal of Comparative Psychology*, *126*, 109–113. http://dx.doi.org/10.1037/a0027758

Price, E. E., & Whiten, A. (2012). Social learning and culture in primates: Evidence from free-ranging and captive populations. In E. A. Wasserman & T. R. Zentall (Eds.), *Handbook of comparative cognition* (pp. 862–878). New York, NY: Oxford University Press.

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Whiten, A., Hinde, R. A., Stringer, C. B., & Laland, K. N. (2011). Culture evolves. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, *366*, 938–948. http://dx.doi.org/10.1098/rstb.2010.0372

APPENDIX 19.2

Animal Social Learning Articles, 2012–2014

Where practicable, each research group/species/behavior combination has a single entry in this table, typically showing the most recent of any multiple relevant publications in this period.

Species	Type	Behavior	Relevant publications
African elephant	C	two-choice	Greco et al., 2013
African elephant	F	crop raiding	Chiyo et al., 2012
Ant	C	nest-site choice	Franklin and Franks, 2012
Baboon	F	foraging	Carter et al., 2014
Baboon	C	pattern recognition	Claidière et al., 2014
Big-eared bat	F	feeding techniques	Geipel et al., 2013
Black bear	F	feeding site	Hopkins, 2013
Blue tit	C	milk-bottle opening	Aplin et al., 2013
Bonobo	F	gestures	Halina et al., 2013
Bottlenose dolphin	F	tool use	Kopps et al., 2014; Mann et al., 2012
Bottlenose dolphin	F	feeding site	Donaldson et al., 2012
Bullfinch	F	feeding innovation	Ducatez et al., 2013
Bumblebee	C	flower choice	Dawson and Chitka, 2012; Leadbetter and Florent, 2014
Bumblebee	C	flower robbing/handedness	Goulson et al., 2013
California mouse	C	paternal behavior	Gleason and Marler, 2013
Chimpanzee	C	imitation recognition	Davila-Ross et al., 2014
Chimpanzee	C	foraging	Buttelmann et al., 2013
Chimpanzee	C	token deposition	Haun et al., 2013
Chimpanzee	C	multiple	Hecht et al., 2013
Chimpanzee	F	multiple	Kamilar and Atkinson, 2014
Chimpanzee	F	tool use	Koops et al., 2013; Luncz and Boesch, 2014; O'Malley, 2012
Chimpanzee	C	tool use	Rawlings et al., 2013
Chimpanzee	C	gesture	Taglialatella et al., 2012
Chimpanzee	C	bodily action	Tennie et al., 2012
Chimpanzee	C	foraging location	Vale et al., 2014
Chimpanzee	C	grass in ear	van Leeuwen et al., 2014
Chimpanzee	C	location choice	van Leeuwen et al., 2014
Chimpanzee	C	using straw to suck	Yamamoto et al., 2013
Chimpanzee	C	making moss sponge	Hobaiter et al., 2014
Chimpanzee	C	habituation to humans	Samuni et al., 2014
Chimpanzee, orangutan	C	foraging	Haun et al., 2014
Convict cichlid	C	predation risk	Barks and Godin, 2013
Cowbird	C	social skills	Gersick et al., 2012
Cuttlefish	C	fear conditioning	Huang and Chaio, 2013
Damselfish	C	predator avoidance	Manassa et al., 2014
Darter spp.	C	mate choice	Moran et al., 2013
Dog	C	do as I do	Fugazza and MiKlosi, 2014
Dog	C	two-action	Pongracz et al., 2012
Fairy wrens	F	brood parasite recognition	Feeney and Langmore, 2013
Fruitfly, adult	C	spatial learning	Foucauld et al., 2013
Fruitfly, larvae	C	food choice	Durisko et al., 2014
Galapagos pelicans	F	location for plunge diving	Brumm and Teschke, 2012
Goffin cockatoo	C	tool use	Auersperg et al., 2014
Golden hamster	C	dominance	Lai et al., 2014
Gorilla, orangutan	F	food choice	Gustafsson et al., 2014
Great tits	F	diversity of song	Feyet et al., 2014

(*Continues*)

APPENDIX 19.2 (*Continued*)

Animal Social Learning Articles, 2012–2014

Where practicable, each research group/species/behavior combination has a single entry in this table, typically showing the most recent of any multiple relevant publications in this period.

Species	Type	Behavior	Relevant publications
Guinea dolphin	F	feeding	Oliviera et al., 2013
Guppy	C	foraging site	Franks and Marshall, 2013
Guppy	C	food richness	Trompf and Brown, 2014
Honeybee	F	foraging site	Balbuena et al., 2012
Horse	C	opening a drawer	Ahrendt, 2012; Krueger et al., 2014
House mouse	C	STFP	Choleris et al., 2013; Ervin et al., 2013
House mouse	C	STFP	Arakawa et al., 2013; Nicol et al., 2014
House mouse	C	food intake	Olszewski et al., 2014
House mouse	C	episodic memory	Lipina and Roder, 2013
Humpback whale	F	feeding technique	Allen et al., 2013
Hyena	F	feeding techniques	Benson-Amram et al., 2014
Japanese quail	C	foraging	Boogert et al., 2013
Killer whale	C	do as I do	Abramson et al., 2012
Lemon shark	C	target contact	Guttridge et al., 2013
Lemur	F	feeding technique	O'Mara et al., 2012; Schnoell et al., 2014
Locust	C	feeding/egglaying	Lancet and Dukas, 2012
Macaque	C	tool use	Macellini et al., 2013
Macaque	C	neonatal lipsmacking	Simpson et al., 2013
Macaque	C	food location errors	Monfardini et al., 2014
Mackerel	C	feeding site	Takahashi et al., 2014a, 2014b
Marmoset	C	foraging	Burkart et al., 2012
Marmoset	C	calls	Watson et al., 2014
Marmoset	F	feeding technique	Gunhold et al., 2014
Medaka	C	movement orientation	Ochiai et al., 2013
Meerkat	F	operate apparatus	Hoppitt et al., 2012; Thornton and Samson, 2012
Mexican guppy	C	mate choice	Bierbach et al., 2012, 2013
Mouse-eared bat	C	foraging site	Clarin et al., 2014
Norway rat	C	fear	Jones et al., 2014
Norway rat	C	fear conditioning	Yusufishaq and Rosenkrantz, 2013
Norway rat	C	drug self-administration	Peitz et al., 2013
Norway rat	C	STFP	Lindeyer et al., 2013
Octopus	C	operant	Tomita and Aoki, 2014
Orangutan	C	tool use	Gruber et al., 2012
Pied flycatchers	F	clutch size	Forsman et al., 2012
Pig	C	STFP	Figuera et al., 2013
Pigeons	F	homing	Pettit et al., 2013
Reed warblers	F	brood parasite recognition	Campobello and Sealy, 2011; Thorogood and Davies, 2012
Ring-billed gull	F	food location	Racine et al., 2012
Root vole	C	food choice	Li et al., 2012
Skink	C	association	Noble et al., 2014
Snake eagle	F	migration route	Panuccio et al., 2012
Sperm whale	F	codas (vocalizations)	Amano et al., 2014
Spider crab, juvenile	C	feeding site	Hanna and Eason, 2013
Squirrel monkey	C	feeding technique	Claidière et al., 2013
Stickleback spp.	C	feeding patch location	Atton et al., 2012, 2014
Stingray	C	operant	Thornhauser et al., 2013
Tent-making bats	F, C	STFP	O'Mara et al., 2014

APPENDIX 19.2 (*Continued*)

Animal Social Learning Articles, 2012–2014

Where practicable, each research group/species/behavior combination has a single entry in this table, typically showing the most recent of any multiple relevant publications in this period.

Species	Type	Behavior	Relevant publications
Titmice spp.	F	nest-site preference	Slagsvold et al., 2013
Trout	C	prey identification	White and Gowan, 2014
Vervet	F	feeding technique	van de Waal et al., 2014
Vultures	F	foraging	Kane et al., 2014
Whooping cranes	F	migration route	Mueller et al., 2013
Wolf/dog	C	feeding site	Range and Viranyi, 2013
Wood frog tadpole	C	predator recognition	Chivars and Ferrari, 2014
Zebra finches	C	song learning	Deshpande et al., 2013
Zebra finches	C	mate choice	Rosa et al., 2012
Zebrafish	C	risk assessment	Zala and Maattanen, 2013
Zebrafish	C	escape aversive stimuli	Vital, 2013
Zebrafish	C	feeding-site preference	Riebel et al., 2012

Note. F = free living; C = captive; STFP = social transmission of food preference.

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