How and Why
Animals Do the
Things They Do

animal
Behavior
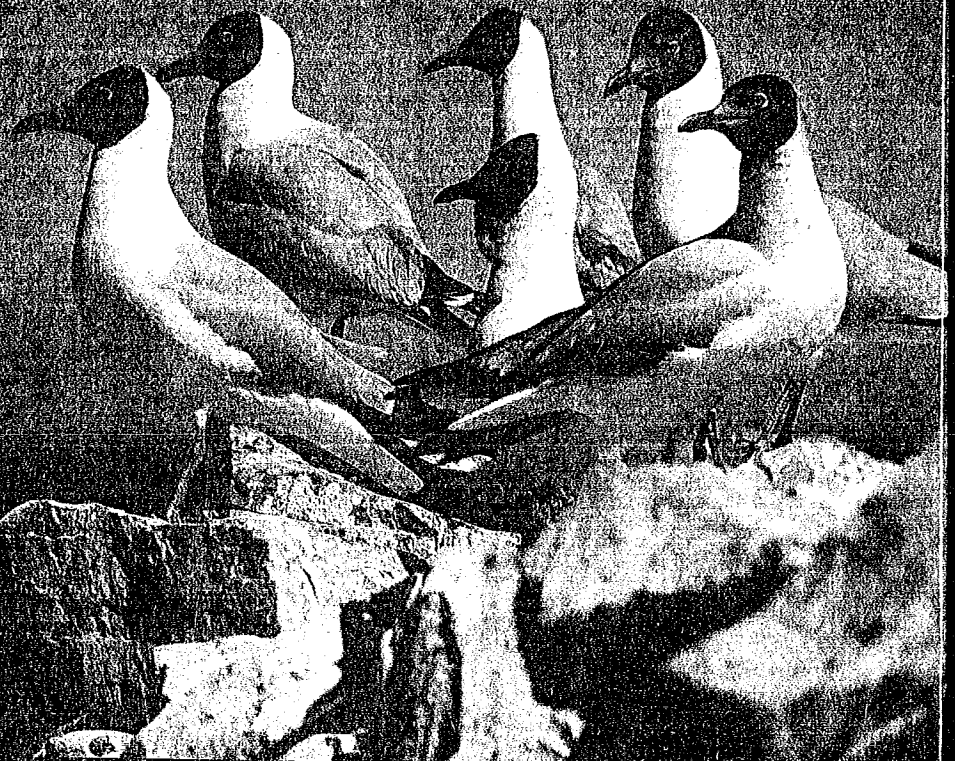
Volume 1 | History, Causation, and Development

Ken Yasukawa and Zuleyma Tang-Martínez, Editors

4

Social Learning, Tradition, and Culture: Data and Debate

Bennett G. Galef

INTRODUCTION

The last three decades have seen a remarkable increase in interest in the possibility that animals' acquisition of adaptive patterns of behavior can be facilitated by their observing the behavior of others. Such *social learning*, as it is often called, is currently seen as playing an important role in animals as diverse as ants and chimpanzees learning almost anything from how to choose a mate to how to handle potentially dangerous prey.

Despite the ever-expanding knowledge of the ways in which social learning affects the development of adaptive behaviors, important questions remain concerning the mechanisms, *functions*, and evolution of social learning. Consequently, in this chapter, I not only review a sample of instances in which social interactions have been clearly shown to influence the ways in which animals come to perform biologically important behaviors but also discuss several aspects of social learning that remain controversial.

EXAMPLES OF SOCIAL LEARNING

It is perhaps best to begin with a few of the many possible examples of phenomena that those who study social learning in animals have examined in detail. More thorough discussions of both the facts of social learning and

controversial issues in the area are available in a number of books and special issues of journals devoted to studies of social learning (e.g., Zentall & Galef, 1988; Heyes & Galef, 1996; Fragaszy & Perry, 2003; Galef & Heyes, 2004; Laland & Galef, 2009; Kendal et al., 2010; Whiten et al., 2011; Nielsen et al., 2012), as well as in innumerable refereed articles in scientific journals, a selection of which are cited in the reference section at the end of this chapter.

Learning How to Court

Brown-headed cowbirds (*Molothus ater*) are particularly interesting subjects for studies of social influence on behavioral development because cowbirds are obligate **brood parasites**. Adult cowbirds always lay their eggs in nests constructed by birds of other species and leave rearing of their young to such foster parents. As a result, early in life, young cowbirds have no opportunity to interact with members of their own species.

In many other species of songbird (see Volume 3, Chapter 2), exposure to the songs of conspecific adult males during a **sensitive period** (see Chapter 9) early in life is necessary if young males are to develop songs that will be attractive to females of their species. Because during this sensitive period in development young male cowbirds do not hear adult males of their species sing, it was long thought that courtship songs of male cowbirds must develop independently of social experience. However, the results of numerous studies by Meredith West and Andrew King and their students (for review, see Freeberg, 2004), have shown that, as in other species of songbird, social learning plays a central role in young males developing songs that will be effective in courting females.

Male cowbirds from different areas of North America sing regional dialects, each a variant of a prototypic cowbird song. These regional dialects are differentially effective in causing females to assume a copulatory posture, with females from each region responding preferentially to the songs of males from that region.

Outside the breeding season, cowbirds live in mixed-sex flocks, and while in these flocks each young male cowbird sings a number of different song variants, ordinarily without immediately repeating any particular song. Female cowbirds respond with a distinctive "wing-stroke" display only to male song variants that will be most effective in causing them to accept a male as a mate during the breeding season. After a female responds to one of a male's songs with a wing-stroke display, the male repeats that song three or four times in succession and increases the frequency with which he subsequently sings it (West & King, 1996). Thus, female cowbirds shape the song displays of males of their species.

.mber of books and special
ing (e.g., Zentall & Galef,
03; Galef & Heyes, 2004;
iten et al., 2011; Nielsen
:icles in scientific journals,
₁ at the end of this chapter.

cularly interesting subjects
ment because cowbirds are
ιy their eggs in nests con-
ιg of their young to such
)irds have no opportunity

₃, Chapter 2), exposure to
itive period (see Chapter
.evelop songs that will be
ιg this sensitive period in
.ult males of their species
:le cowbirds must develop
sults of numerous studies
ents (for review, see Free-
⁻ songbird, social learning
;s that will be effective in

rica sing regional dialects,
egional dialects are differ-
:opulatory posture, with
⊃ the songs of males from

xed-sex flocks, and while
umber of different song
y particular song. Female
lisplay only to male song
⊃ accept a male as a mate
to one of a male's songs
ng three or four times in
he subsequently sings it
he song displays of males

The songs of male cowbirds that are most effective in eliciting positive responses from females are also the songs that most frequently elicit attacks by other male cowbirds, causing submissive males to abandon singing highly effective songs. As a result, only the dominant males in a group can continue to produce song variants that have a high probability of eliciting positive responses from females, and females therefore have a high probability of mating with socially dominant males.

Learning Where, What, and How to Eat

Perhaps the most thoroughly investigated instances of social learning are those influencing development of various aspects of foraging (e.g., choice of foods and feeding sites, methods of exploiting heavily defended foods, etc.). Consequently, examples of social influences on foraging behaviors—ranging from the development of flavor preferences in Norway rats (*Rattus norvegicus*) to the methods that chimpanzees (*Pan troglodytes*) use to feed on army ants— are scattered throughout this chapter.

The relative frequency of studies of social influences on various aspects of foraging behavior reflects both the considerable time and energy that members of many species spend acquiring food and the resultant ease with which feeding behaviors can be studied in both captive and free-living animals. Further, because the feeding behavior of wild rodents has a substantial impact on human success in producing food, and because many rodents (e.g., rats, mice, hamsters, voles, etc.) thrive in captivity (where behavior can be most easily studied under controlled conditions), progress in analysis of social influences on the foraging behavior of rodents (and of honey bees, which share both characteristics [see Chapter 12; von Frisch, 1967]) has progressed relatively rapidly. Here, the focus is on social influences on the feeding of rodents, though a similar review could be provided with respect to social effects on foraging in avian species (e.g., Galef & Giraldeau, 2001).

Social influences on foraging in rats—More than a half-century ago, von Fritz Steiniger (1950), an applied ecologist, tried various ways to decrease the cost of controlling pest populations of Norway rats. One tactic Steiniger evaluated involved introducing large portions of poison bait into a rat-infested area, thus avoiding some of the expense associated with the usual procedure of constantly replenishing small portions of bait as rats consumed them. Much to his dismay, Steiniger found that despite initial reduction in rat numbers shortly after he introduced a large portion of bait into a rat-infested area, the target population soon completely stopped eating the poisoned bait and eventually returned to its initial size. The reasons for this failure to provide long-term reduction in rat numbers proved interesting.

First and most obviously, although most rats in a target population ingested a lethal dose of poison when it was first introduced, a few ate less than a lethal amount of bait, became ill, and learned, as a result of that single experience with the poisoned bait, to avoid further ingestion of it (Garcia & Koelling, 1966). Second, and far more discouraging to Steiniger, young rats born to survivors of initial contact with a poisoned bait totally rejected that bait without ever even tasting it. Bait avoidance learned by surviving rats appeared to be somehow transmitted to their young.

Mertice Clark and I (Galef & Clark, 1971a) brought adult wild rats captured on garbage dumps into the laboratory, established the rats in small colonies, and offered them two foods, one of which we had contaminated with a mild toxin. As expected, the captive rats rapidly learned to eat only the untainted food and continued for weeks to avoid the previously tainted food even when provided with untainted samples of it. Further, as Steiniger had found, young subsequently born to such trained colonies refused to even taste the previously tainted food that the adults of their colony had learned to avoid (Galef & Clark, 1971a).

Because the phenomenon of social transmission of bait avoidance could be studied under controlled conditions, investigation of social-learning processes leading to transmission of food choices from adult rats to their offspring became possible, and several different types of interaction between young and adult rats were found to result in transmission of learned food preferences from adult rats to their offspring (for review, see Galef, 1985).

Selecting a place to eat—Young wild rats emerging from their nest site to take their first meals of solid food use visual cues to find adults at a distance from the nest (blind rat pups do not show the effect) and approach them (Galef & Clark, 1971b). In fact, placing an anesthetized adult rat in the vicinity of one of two otherwise identical feeding sites leads pups to both visit and feed at the site close to the anesthetized rat far more frequently than at the alternative (Galef, 1981).

Indeed, adult rats do not even have to be present at a feeding site to increase its attractiveness to their young. As adult rats leave a feeding site and return to their nest, they deposit scent trails that young rats follow when seeking food (Galef & Buckley, 1996). Furthermore, while feeding, rats defecate and urinate in the area where they eat, and these residual cues, like the actual presence of an adult at a feeding site, attract pups and cause them to eat in locations that adults have exploited (Galef, 1985; Laland & Plotkin, 1990).

Of course, in natural circumstances foods are often patchily distributed. Consequently, learning to eat in a location where adults have eaten often leads to eating a food that adults have eaten.

ı target population ingested
, a few ate less than a lethal
lt of that single experience
ı of it (Garcia & Koelling,
ger, young rats born to sur-
ᵣ rejected that bait without
·viving rats appeared to be

) brought adult wild rats
stablished the rats in small
we had contaminated with
ly learned to eat only the
he previously tainted food
Further, as Steiniger had
lonies refused to even taste
olony had learned to avoid

of bait avoidance could be
ɔf social-learning processes
ılt rats to their offspring
teraction between young
ɔf learned food preferences
ılef, 1985).

ng from their nest site to
ɔ find adults at a distance
fect) and approach them
ized adult rat in the vicin-
ıds pups to both visit and
ɔre frequently than at the

ıt a feeding site to increase
feeding site and return to
ɔllow when seeking food
ng, rats defecate and uri-
ɔs, like the actual presence
em to eat in locations that
n, 1990).
ˀten patchily distributed.
ılts have eaten often leads

Selecting a food to eat—Even before birth, young rats can obtain information from their mother concerning at least some of the foods that she has eaten while gestating them. Peter Hepper (1988) fed garlic to pregnant rats and then, shortly after garlic-fed mothers delivered their litters, transferred the young to foster mothers that had never eaten garlic. When subsequently offered a choice between dishes containing garlic and onion, pups that had been gestated by a mother eating garlic spent more time near the dish containing garlic than pups gestated by mothers not exposed to garlic. Similarly, Smotherman (1982) found that injecting lemon flavor into the amniotic fluid of a rat mother resulted in her offspring, when adult, increasing their preference for lemon-flavored food.

The flavor of foods that a dam eats affects not only the flavor of her amniotic fluid but also the flavor of her milk. At weaning, rat pups prefer foods with flavors that they have experienced in their mother's milk (for review, see Galef, 1985).

My students and I have also found that after a naïve young rat (an observer rat) interacts for a few minutes with an adult rat that has recently eaten a distinctively flavored food (a demonstrator), the observer rat shows a markedly enhanced preference for whatever food its demonstrator ate (for review, see Galef, 1988, 1996). Similar effects have been found in other mammalian species ranging from bats (Ratcliffe & ter Hofstede, 2005) to hyenas (Yoerg, 1991).

Analyses of the processes underlying this last type of social induction of flavor preference have repeatedly shown that, if an observer rat is to develop a preference for the food that its demonstrator ate, the observer rat has to experience the odor of a food at the same time that it experiences the breath of a demonstrator rat. Simple exposure to a food odor in isolation does not produce the effect.

Chemical analysis of rat breath reveals significant concentrations of carbon disulfide (CS_2), and experiments show that experience of a food odor together with CS_2 results in enhanced preference for the food almost as great as experience with a demonstrator rat that has eaten that food (Galef, 1988). Further, recent electrophysiological studies of the olfactory system of mice have revealed a specialized olfactory subsystem expressing the receptor guanylyl cyclase that is highly sensitive to CS_2. Gene-targeted mice with disruptions of the transduction cascade that transforms receptor response to CS_2 into electrical impulses in the nervous system not only lose sensitivity to CS_2 but also fail to show social influences on their food choices (Munger et al., 2010). Thus, there appears to be a specialized portion of the olfactory system in mice (and presumably other rodent species as well) dedicated to social learning of food preferences.

Learning How to Eat

There are no squirrels in the pine forests of either Israel or Corsica, and consequently there are no specialized mammals present in these forests eating pine seeds, the sole food suitable for mammals found there. In both Israel and Corsica, and nowhere else, roof rats (*Rattus rattus*) have learned to eat pine seeds and have established colonies that have thrived in pine forests for many generations (Terkel, 1996).

Laboratory studies of the feeding behavior of rats captured in pine forests in Israel reveal that in order for rats to gain more energy from eating pine seeds than they expend in removing the tough scales that protect the seeds from potential predators, the rats must take advantage of the physical structure of the pinecones, first removing scales from the base of a cone and then removing in succession the spiral of scales circling a cone's shaft from base to apex.

Almost all young rats reared by either their natural mother or a foster mother who efficiently stripped the scales from pinecones while young were present acquire the efficient technique. To the contrary, young rats reared by either their natural mother or a foster mother that does not know how to open pinecones efficiently almost never learn to open pinecones efficiently for themselves.

The failure of young rats reared by dams that do not strip cones efficiently to learn to open pinecones efficiently and the success of young rats reared by dams that do strongly suggest that the behavior of mothers somehow facilitates young rats learning to strip pinecones of their seeds. Indeed, further studies showed that the experience of young rats completing the stripping of scales from cones properly started by an adult rat allowed most young rats to acquire the efficient method, even if the young were reared by a female rat that did not know how to open cones efficiently. Most informative, a majority of young rats reared by a dam who did not strip cones efficiently and given access to cones started by a human experimenter (who had used a pair of pliers to remove a few scales from the base of cones) also learned the efficient technique (Terkel, 1996).

The type of social learning involved in learning to strip pinecones of their seeds is not particularly sophisticated. It involves nothing more than directing the attention of young rats to the base of cones. Nonetheless, such simple social learning is sufficient to establish a tradition of pinecone opening in roof rats that allows them to thrive in a portion of the environment that would otherwise be closed to them.

Learning to Attack "Toxic" Prey

Food choices can be socially influenced by exposure not only to olfactory and visual cues but to acoustic cues as well. The group nesting, socially

her Israel or Corsica, and
sent in these forests eating
d there. In both Israel and
) have learned to eat pine
d in pine forests for many

captured in pine forests in
gy from eating pine seeds
at protect the seeds from
: the physical structure of
a cone and then removing
ift from base to apex.
mother or a foster mother
while young were present
oung rats reared by either
· know how to open pine-
efficiently for themselves.
ot strip cones efficiently to
young rats reared by dams
omehow facilitates young
d, further studies showed
pping of scales from cones
its to acquire the efficient
that did not know how to
of young rats reared by a
cess to cones started by a
remove a few scales from
(Terkel, 1996).
) strip pinecones of their
hing more than directing
onetheless, such simple
binecone opening in roof
ronment that would oth-

ire not only to olfactory
group nesting, socially

foraging, neotropical fringe-lipped bat (*Trachops cirrhoses*) is unique among bats in using the calls that male frogs use to attract mates to locate potential food (Tuttle & Ryan, 1981). Most other species of bat use their sonar to detect prey rather than using the sounds made by prey to locate and capture them.

In the wild, fringe-lipped bats prey frequently on túngara frogs (*Physalaemus pustulosus*) and avoid contact with poisonous cane toads (*Bufo marinus*). When brought into the laboratory for study, recently captured, hungry fringe-lipped bats readily approach a concealed loudspeaker playing the mating calls of túngara frogs but avoid one playing the easily distinguished mating calls of cane toads.

Rachel Page and Michael Ryan (2006) captured fringe-lipped bats and exposed them to a series of trials in which the bats were rewarded with food when they approached a concealed loudspeaker playing an artificial call made by electronically combining a cane-toad call with that of a túngara frog. Over trials, Page and Ryan (2006) gradually decreased the loudness of the frog-call portion of the compound auditory stimulus while gradually increasing the loudness of its toad-call portion until hungry bats would fly for food to a loudspeaker broadcasting pure toad calls.

Once a bat had been trained to approach cane-toad calls, it was placed together with a second fringe-lipped bat that had been captured and then tested for its response to a loudspeaker broadcasting cane-toad calls (none responded positively). This second bat was then allowed to observe the trained bat fly to and acquire food at the concealed speaker playing cane-toad calls.

Observer bats quickly began to fly to loudspeakers playing cane-toad calls and could subsequently be used as demonstrators for other wild-caught bats that initially avoided cane-toad calls. It is easy to imagine that such social learning could help fringe-lipped bats track the rapid seasonal changes in the availability of various prey species of frog typical of neotropical rain forest.

Learning Where to Nest

Information contained in the behavior of knowledgeable individuals is likely to be of greater value than information obtained by observing the less well informed (Laland & Galef, 2009). Consequently, in some circumstances, natural selection seems to have acted to predispose animals to learn socially from members of species other than their own.

Blue tits (*Parus caeruleus*) and great tits (*Parus major*)—both close relatives of North American chickadees—as well as pied flycatchers (*Ficedula hypoleuca*) living in northern Europe nest in holes in tree trunks (or in suitable nest boxes provided by humans). During the nesting season, all three species forage on

similar foods, fall prey to similar predators, and utilize similar nesting sites. The tits are year-round residents, but the flycatchers come to Europe only to breed in the spring and summer. Consequently, the tits are likely to be well informed as to local conditions, and migrant flycatchers might obtain useful information from the tits when selecting locations in which to nest and rear their young.

During the winter, Janne-Tuomas Seppanen and Jukka Forsman (2007) provided great and blue tits in eight locations with an excess number of nest boxes. Further, before the flycatchers arrived in the spring, the experimenters decorated all the nest boxes in each area in which the tits had chosen to nest with either a circle or square so that it would appear to arriving migrant fly-catchers that all tits in an area had chosen nest sites marked with one symbol or the other. Also, before the flycatchers arrived, the experimenters placed a second nest box a few meters from each nest box the tits were occupying and marked the second nest box with the opposite symbol so that it would look to arriving flycatchers as though tits were avoiding nest sites with that mark.

When the first flycatchers arrived on the study sites in spring, the experimenters placed pairs of empty nest boxes, one marked with a triangle and one marked with a circle, in each of the eight study sites so that arriving fly-catchers could choose between them. The flycatchers clearly preferred nest boxes of the same type apparently preferred by tits in their area and by late in the mating season were three times as likely to nest in this type of nest box as in the other. Male flycatchers were seen to visit tits' nests early in the breeding season, and information gathered during these visits may have played a role in providing the flycatchers with information (Forsman & Thomson, 2008).

Learning What to Fear

Recognizing and responding appropriately to potential predators is a challenge many birds and mammals face, and given the range of predators that prey especially on smaller species, innate recognition of each potentially predatory species is not likely. In vertebrates ranging from European blackbirds (*Turdus merula*; Curio, 1988) to Japanese macaques (*Macaca fuscata*; Mineka & Cook, 1988), naïve individuals learn to respond to potential predators by attending to the behavior of knowledgeable individuals (reviewed in Griffin, 2004).

Although we tend to think of flight or concealment as the most appropriate response to the appearance of a potential predator, many species of bird respond to potential predators with a behavior known as *mobbing*. When mobbing, an individual discovering a predator produces a special vocalization

:e similar nesting sites.
ome to Europe only to
its are likely to be well
:rs might obtain useful
which to nest and rear

ukka Forsman (2007)
excess number of nest
:ing, the experimenters
tits had chosen to nest
o arriving migrant fly-
arked with one symbol
:rimenters placed a sec-
:s were occupying and
l so that it would look
sites with that mark.
: in spring, the experi-
:d with a triangle and
:es so that arriving fly-
clearly preferred nest
their area and by late
st in this type of nest
tits' nests early in the
visits may have played
'orsman & Thomson,

ial predators is a chal-
inge of predators that
:ach potentially preda-
European blackbirds
lacaca fuscata; Mineka
potential predators by
; (reviewed in Griffin,

s the most appropriate
many species of bird
n as *mobbing*. When
; a special vocalization

(a *mobbing call*), and begins to behave aggressively toward (mob) the preda-
tor. Other birds approach and join in (hence the term *mobbing*), both giving
mobbing calls and attacking the predator. Owls frequently prey on European
blackbirds, and when they see an owl, wild-caught, adult blackbirds give mob-
bing calls and harass the potential predator.

Using a simple but ingenious apparatus in which demonstrator and
observer blackbirds were separated by an opaque barrier, Curio (1988) allowed
an experienced blackbird to look at a stuffed owl and direct mobbing calls
towards it while a naïve blackbird looked at a stuffed, harmless (nonpredatory)
bird. In response to the mobbing vocalizations of the experienced bird looking
at the owl, the naïve bird started to give mobbing vocalizations of its own and
to act aggressively, but towards the harmless object at which it was looking,
not towards the owl that was invisible to it.

Days later, when the previously naïve bird was again shown the stuffed,
harmless bird, it gave mobbing vocalizations and attacked it. Indeed, this pre-
viously naïve bird had learned so well that it could now serve as a model for a
new naïve bird, inducing it also to mob the harmless object. Curio was thus
able to establish a tradition of mobbing a harmless stuffed bird in a captive
population of blackbirds.

Recent field studies by Heather Cornell and colleagues (2011) provide evi-
dence of similar social learning of mobbing responses both within and
between generations of American crows (*Corvus brachyrhyncos*) living outside
the laboratory. Individual marked crows that had been trapped, banded,
and released by an experimenter wearing a distinctive mask gave mobbing
vocalizations to the masked figure and attracted other crows. Both other adult
crows and offspring of the banded crows subsequently mobbed any human
wearing the distinctive mask while not mobbing individuals wearing a
different mask.

Learning with Whom to Mate

Sampling among potential mates to decide which of many potential part-
ners would make the best parent for one's offspring can be an expensive
undertaking, both consuming time and energy that could be devoted to other
activities and increasing the risk of predation on individuals focused on evalu-
ating mates. Information that might reduce such costs can be valuable.

Lee Dugatkin (1996) was the first of several investigators to examine the
possibility that animals, especially those that are young and inexperienced in
such matters, might copy the mate choices of others, thus both reducing the
potential cost associated with identifying an appropriate mate and taking ad-
vantage of experienced individuals' possibly superior knowledge. If you copy

someone else's choice of a partner, you will do no worse than they did while avoiding any potential costs of evaluating potential mates.

Dugatkin and colleagues worked with laboratory-born descendants of wild guppies (*Poecilia reticulata*), a small freshwater fish familiar to all aquarium keepers. Guppies were an appropriate choice for such experiments because in their natural habitat (streams in Trinidad, where Dugatkin captured them) guppies select partners and breed under conditions that would allow them to observe and copy one another's mate choices.

Dugatkin conducted his experiments with guppies in a simple apparatus consisting of a large aquarium placed between two smaller aquaria. He positioned a male "target" guppy in each of the small aquaria and a "focal" female guppy, restrained in a transparent tube, in the middle of the central aquarium. He then introduced a second female (a "model" female) into one of the two smaller aquaria but separated from the target male by a transparent barrier.

The focal female, constrained in the transparent tube in the central aquarium, then watched while one of her target males courted the model female and the other remained alone. Dugatkin then removed the model female from the apparatus, released the focal female from the tube constraining her, and allowed her to choose between her two target males. Seventeen of 20 focal females tested in this way spent more time near the target male they had seen courting a model female than near the target male that had remained alone.

Although this result is surely consistent with the hypothesis that female guppies copy one another's choices of partner, it is also possible that female guppies, members of a species that gathers in shoals in nature, simply prefer a place where they have previously seen two fish to a place where they have seen only one fish or that the behavior of a male who has recently courted is different from and more attractive to females than that of a male that has not, and so forth. Experiments to test such alternative explanations are easy to carry out, and their outcomes allowed Dugatkin to exclude many such alternative explanations of the females' preferences for males they had seen courting other females. Female guppies, like females of some other species of fish, as well as of some avian species, prefer to mate with individuals that they have seen courting others (for review, see White, 2004).

Such laboratory evidence of a tendency to copy the mate choices of conspecifics suggests an explanation for some unusual behavior seen in species (e.g., sage grouse [*Centrocercus urophasianus*] or prairie chickens [*Tympanuchus cupido*]) in which males compete for females on communal breeding grounds (*leks*) that females visit for no purpose other than to choose a male and mate. Often, only a small percentage of the males on any lek get to mate, and these fortunate males each mate with many female visitors.

worse than they did while
mates.

-born descendants of wild
familiar to all aquarium
:h experiments because in
Dugatkin captured them)
that would allow them to

ies in a simple apparatus
smaller aquaria. He posi-
uaria and a "focal" female
e of the central aquarium.
male) into one of the two
y a transparent barrier.
tube in the central aquar-
:ourted the model female
ed the model female from
ibe constraining her, and
es. Seventeen of 20 focal
target male they had seen
hat had remained alone.
ie hypothesis that female
also possible that female
s in nature, simply prefer
a place where they have
10 has recently courted is
n that of a male that has
tive explanations are easy
in to exclude many such
; for males they had seen
s of some other species of
with individuals that they
04).

e mate choices of conspe-
ivior seen in species (e.g.,
chickens [*Tympanuchus*
imunal breeding grounds
choose a male and mate.
ek get to mate, and these
.

Human investigators have been unable to identify characteristics that differentiate successful from unsuccessful males on a lek. However, if females in lekking species copy one another's mate choices, as laboratory findings of mate-choice copying in other avian species suggest they may (Galef, 2009), then the extreme skew in female choice of male partners is not difficult to understand. Indeed, the observed sequence of mating behavior on sage-grouse leks is consistent with the hypothesis that female grouse observe and copy one another's mate choices, thus producing the observed inequality in male success (Gibson et al., 1991).

DEFINING TYPES OF SOCIAL LEARNING: THE ANALYSIS OF BEHAVIOR

The preceding examples provide evidence of effects of socially acquired information on the behavior of many species in many circumstances. However, as a moment's reflection about such examples makes clear, social learning can occur in quite different ways. There have been many attempts to both categorize the behavioral processes involved in social learning (for examples, see Galef, 1988; Whiten & Ham, 1992; Heyes, 1994; Zentall, 1996) and to determine the type of social learning processes responsible for particular instances of social influence on behavior.

Sometimes an animal actively shapes the behavior of another (for example, when female cowbirds give a wing stroke in response to a male's song). As illustrated below, sometimes social learning appears to involve true imitation (learning to do a motor act from seeing another perform that act; Thorndike, 1898). In other cases, social learning appears to rest on emulation—learning by watching others that a goal can be achieved without learning very much about the behavior a knowledgeable individual used to achieve the goal (Tomasello, 1994).

As we have seen in many of the examples discussed above (for example, when rats deposit olfactory cues at a feeding site), local enhancement ("apparent imitation resulting from directing the animal's attention to a particular object or part of the environment" [Thorpe, 1963, p. 134]) often suffices to increase the probability that a naïve animal will come to exhibit the same behavior as others of its social group.

Why should we make the effort to distinguish among processes involved in social learning? It can be argued that all social learning processes serve similar functions, for example, permitting animals to learn adaptive behaviors without incurring whatever costs are involved in learning for oneself by trial and error. Fine-grain distinctions differentiating local enhancement from emulation and emulation from imitation may seem an unnecessary burden. However, there are contexts in which such distinctions have proven useful.

One of the important questions faced by those interested in social learning is why social learning has resulted in impressive cumulative cultures in the human species but not in any other. All agree both that nonhuman animals exhibit socially learned behavioral traditions and that these traditions never approach the level of sophistication and complexity of the cultures seen in all human social groups. *Is it because the processes supporting social learning in humans differ from those seen in other animals?*

As discussed more fully in the section of this chapter concerned with animal culture, experts have both asserted (e.g., Galef, 2009; Tomasello, 2009) and denied (e.g., Heyes, 1993) that an ability to imitate or teach is critical for production of the kind of cumulative culture typical of human societies. However, if cumulative culture does depend on an ability to teach or imitate, the question of whether animals in general, and chimpanzees and orangutans in particular, engage in teaching or imitation becomes central to our understanding of the obvious difference in the extent and complexity of the traditions exhibited by our own species and by other animals, even our closest relatives.

The only distinctions used in the remainder of this chapter involve determining, first, whether, in any particular instance, a naïve individual (1) acquires by observation a pattern of behavior exhibited by another (imitates); (2) has its attention directed towards important aspects of the environment or environmental affordances by the behavior of others (for example, as a result of local enhancement or emulation) and then learns for itself how to achieve a desired outcome; or (3) whether knowledgeable individuals modify their behavior in the presence of naïve individuals and thus facilitate acquisition of behavior by pupils (*teaching*). In cases of imitation, emulation, and local enhancement, naïve individuals extract useful information as a result of observing the normal behavior of accomplished individuals, whereas in teaching, the knowledgeable individual behaves differently in the presence than in the absence of a naïve individual, thus both facilitating learning by pupils and incurring some cost from teaching (Caro & Hauser, 1992).

The distinctions being made may be clarified by a hypothetical example. Consider an adolescent chimpanzee watching its mother as she uses her left hand to lift a log and then takes insect larvae from the log's underside with her right hand. The juvenile chimp might learn from watching its mother (1) to investigate the log (local enhancement), (2) to look for food by turning over logs (emulation), or (3) to put its left hand under a log, move that hand upward, and pick up food with its right hand (imitation). If the mother chimp were to slow or exaggerate her movements when her infant was present (thus sacrificing efficiency), allowing her "pupil" to learn to find grubs under logs sooner than it would have by simply watching its mother hunt for grubs in

nterested in social learning
umulative cultures in the
h that nonhuman animals
:hat these traditions never
· of the cultures seen in all
porting social learning in

ıter concerned with animal
)9; Tomasello, 2009) and
or teach is critical for pro-
ɔf human societies. How-
ty to teach or imitate, the
ʼanzees and orangutans in
central to our understand-
mplexity of the traditions
even our closest relatives.
:his chapter involve deter-
:e, a naïve individual (1)
ited by another (imitates);
:pects of the environment
others (for example, as a
ɛn learns for itself how to
geable individuals modify
ınd thus facilitate acquisi-
mitation, emulation, and
information as a result of
ividuals, whereas in teach-
:ly in the presence than in
tating learning by pupils
ıuser, 1992).

y a hypothetical example.
ıother as she uses her left
ı the log's underside with
ʼom watching its mother
ɔ look for food by turning
der a log, move that hand
:ion). If the mother chimp
:r infant was present (thus
ı to find grubs under logs
mother hunt for grubs in

the normal way, then teaching would be involved. Specific, real examples of the more complex forms of social learning (teaching, imitation, emulation) are discussed in the next few paragraphs.

Teaching

As mentioned above, teaching differs from other types of social learning in that, when teaching, a teacher suffers some short-term cost (e.g., a loss of efficiency or delay or loss of reward) with the result that a pupil acquires some behavior more rapidly than it would have if it weren't taught (Caro & Hauser, 1992). In most social-learning processes involving a knowledgeable demonstrator and naïve observer, it is the behavior of the observer that changes. In teaching both the demonstrator's and the observer's behaviors change (Hoppitt et al., 2008).

There has been some question as to the importance of teaching even in human preindustrial societies (Laland & Hoppitt, 2003), and, of course, it is inappropriate in the absence of careful studies to assume that we somehow know how hunter-gatherers acquire skills. Perhaps surprisingly, less is known of the role of social learning in the acquisition of life skills by humans than by many other animals, and formal, language-based instruction of the kind typical in industrial societies seems to be rare in the preindustrial world. Still, recent anthropological observations suggest that teaching, as defined in the preceding paragraph (Caro & Hauser, 1992), plays an important role in maintenance of the complex behavioral traditions that are characteristic of human populations in pre- as well as postindustrial societies (e.g., Ruddle & Chesterfield, 1997; Diamond, 2001).

Although a handful of possible instances of teaching by apes and cetaceans have been provided in the literature, many find these examples relatively unconvincing (for review, see the discussion of Rendell & Whitehead, 2001). Perhaps most interesting, with the exception of two instances of possible of adult chimpanzees teaching their young to crack nuts (Boesch, 1991), there have been no reports of teaching in free-living chimpanzees or bonobos (*Pan paniscus*) despite tens of thousands of hours of observation. Consequently, recent reports of teaching in animals with much less sophisticated nervous systems than those of great apes, whales, or porpoises, far exceeding the criteria for teaching proposed by Caro and Hauser (1992), came as something of a surprise (for review, see Thornton & Raihani, 2008).

Perhaps the most compelling case of teaching in a nonhuman species involves wild meerkats (*Suricata suricatta*). Young meerkats are largely dependent on the adult members of their colony for sustenance, although by the

time young are three months of age, they can forage for themselves, handling a variety of prey, including potentially dangerous scorpions.

Observations of free-living meerkats, together with experimental interventions in wild populations, show that the transition to nutritional independence is facilitated by adults teaching the young necessary skills (Thornton & McAuliffe, 2006). Normally, adults consume whatever prey they capture. However, when in the presence of begging young, adults often kill or disable prey (scorpions are disabled by removing their stingers), then carry the food to juveniles.

As pups become older and more experienced at handling scorpions, adults give the young intact scorpions increasingly often. Apparently, adults judge the ability of young to handle scorpions from the maturity of their begging calls, and playing recordings of begging calls of older pups to adult meerkats providing scorpions to younger individuals causes the adults to bring intact scorpions, even though the young being fed are not yet ready to handle such dangerous items. Conversely, playing recordings of the calls of young pups to adults provisioning older individuals causes adults to increase the frequency with which they deliver disabled scorpions to older pups.

Further, as the Caro and Hauser (1992) definition of teaching requires, the provisioning strategy of adult meerkats accelerates the acquisition of scorpion-handling skills by juveniles. Pups given disabled scorpions by a human experimenter learned to handle intact scorpions effectively at a younger age than pups that had been artificially provisioned with either dead scorpions or hard-boiled eggs.

Lest you think that teaching is confined to big-brained mammals, it is worth looking closely at such phenomena as the waggle dance of the honey bee (see Chapter 12) and tandem running in ants, where successful foragers guide their nest mates to newly discovered food sources (Franks & Richardson, 2006). When in the company of a naïve nest mate, an ant of the species *Temnothorax albipennis* that knows the location of a food source moves slowly toward it, travelling in spurts and pauses. During such tandem runs to food, the leader slows its pace, waiting while the follower looks around, apparently to examine landmarks, and the leader moves rapidly toward food only after its follower taps it with its antennae. The result of this unusual behavior is that a leader ant sacrifices efficiency in returning to food (an ant acting as leader of a nest mate takes four times as long to travel to food as it would if it were travelling to food alone), while followers show clear benefits from following, both finding food far faster when following a leader than when searching on their own and returning more directly to their nest than did their leader after its initial discovery of food.

)rage for themselves, handling a
s scorpions.

ier with experimental interven-
.sition to nutritional indepen-
ing necessary skills (Thornton
ne whatever prey they capture.
ing, adults often kill or disable
r stingers), then carry the food

d at handling scorpions, adults
iften. Apparently, adults judge
. the maturity of their begging
if older pups to adult meerkats
iuses the adults to bring intact
:e not yet ready to handle such
ngs of the calls of young pups
adults to increase the frequency
ilder pups.

inition of teaching requires, the
ites the acquisition of scorpion-
d scorpions by a human experi-
'ectively at a younger age than
with either dead scorpions or

:o big-brained mammals, it is
the waggle dance of the honey
ants, where successful foragers
id sources (Franks & Richard-
iest mate, an ant of the species
i of a food source moves slowly
'ing such tandem runs to food,
lower looks around, apparently
rapidly toward food only after
of this unusual behavior is that
food (an ant acting as leader of
food as it would if it were trav-
.r benefits from following, both
r than when searching on their
han did their leader after its ini-

Imitation

Interest in the possibility that animals are able to imitate, defined as learning to do an act from seeing it done (Thorndike, 1898), dates to the late nineteenth century when George Romanes (1884), a disciple of Charles Darwin, provided anecdotal observations consistent with the view, widely held at the time, that animals could acquire complex patterns of behavior by observing and then imitating the activities of either humans or members of their own species. Late in the nineteenth century, the view that animals could imitate was challenged by Edward Thorndike (1898), an early comparative psychologist, who was the first to examine the ability of animals to imitate under controlled conditions.

Thorndike studied the ability of his subjects to learn, from observing trained demonstrators, how to escape from various "puzzle boxes" that required hungry animals to make simple responses (e.g., pull a string or step on a lever) to gain access to food. Thorndike's failure to find evidence that cats, dogs, or chickens could learn such simple acts by watching trained conspecifics demonstrate them led him to conclude that animals cannot imitate.

Imitation in animals was of great interest because an ability to imitate was seen as indicating the presence of complex cognitive abilities (though more recently that view has been challenged; see Heyes, 1994, 2012). Consequently, subsequent generations of students of animal learning found Thorndike's failure to provide evidence of imitation in animals an irresistible challenge, and for 90 years innumerable experiments were undertaken using more sophisticated versions of Thorndike's puzzle boxes in the attempt to demonstrate that animals could, in fact, "from an act witnessed, learn to perform that act" (Thorndike, 1911, p. 79) and were therefore capable of complex forms of mental activity.

However, it proved impossible using methods akin to Thorndike's to exclude the possibility that some less cognitively demanding social learning process (such as local enhancement) was responsible for any facilitation of naïve animals' acquisition of a behavior that it had seen demonstrated by a trained conspecific. For example, in a typical study (and one that was widely cited at one time as demonstrating learning by imitation), kittens given an opportunity to observe their mother pressing a lever to obtain food subsequently learned to press the lever far more rapidly than kittens that had watched a strange female press the lever for food. The data can be interpreted as showing either that (1) kittens imitate their mothers or (2) mother cats are better than unfamiliar adult cats at calling their kittens' attention to some portion of the environment. Not surprisingly, all serious discussions found

evidence of imitation provided by the results of such studies relatively unconvincing (for review, see Galef, 1988).

The two-action method—Persuasive evidence of imitation in animals became available only in the latter part of the twentieth century, some decades after it was first found that a naïve bird (an observer) that had watched a trained bird (a demonstrator) use either its foot or bill to depress a lever and obtain food tended to use the same appendage to press the lever as had its demonstrator (Dawson & Foss, 1965). The power of this **two-action method** lay in the fact that demonstrators directed different behaviors toward the same object and location, making it impossible to attribute any tendency of observers to copy the behaviors of their respective demonstrators to local enhancement.

Introduction of the two-action method resulted in a dramatic change in the experimental paradigm used to study imitation learning. Observer pigeons and quail watched others of their species either step on or peck at treadles; observer starlings watched as other starlings pulled or pushed at stoppers concealing food (for review, see Zentall, 2004); observer chimpanzees and children watched adult humans as they pushed or pulled at stoppers blocking access to food in artificial fruit (for review, see Whiten et al., 2004). Results of such studies provided convincing evidence that a surprising range of avian and mammalian species could imitate simple behaviors, and, consequently, that contrary to the conclusion Thorndike (1911) had reached, many animals could learn to do an act from seeing it done.

Diffusion chain experiments—The two-action method has been widely used in **diffusion-chain** laboratory experiments to produce behavioral traditions in groups of animals that are similar in important respects to the traditions seen in human social groups. In a diffusion-chain experiment (we have already seen examples in Curio's work on social transmission of mobbing in blackbirds and Page and Ryan's work with fringe-lipped bats) in which imitation is involved, a demonstrator that has been explicitly trained to exhibit one of two behaviors directed toward some object is observed by a naïve individual. When the originally naïve individual acquires the behavior that its trained demonstrator exhibited, it becomes a demonstrator for a second naïve individual, and the process is repeated, potentially indefinitely (e.g., Dindo et al., 2008). The ability of apes to faithfully transmit behaviors across cultural generations in diffusion-chain studies suggests that they, like humans, may be bearers of **culture** (for review, see Whiten, 2009), the subject of the final section of this chapter.

Do this—A second method used to explore the possibility that animals are able to imitate involves first training subjects to repeat arbitrary actions

h studies relatively uncon-

: of imitation in animals
ieth century, some decades
:rver) that had watched a
 bill to depress a lever and
) press the lever as had its
of this *two-action method*
 behaviors toward the same
ite any tendency of observ-
 demonstrators to local

in a dramatic change in the
:arning. Observer pigeons
:ep on or peck at treadles;
 or pushed at stoppers con-
ver chimpanzees and chil-
ulled at stoppers blocking
niten et al., 2004). Results
a surprising range of avian
aviors, and, consequently,
had reached, many animals

:thod has been widely used
duce behavioral traditions
t respects to the traditions
xperiment (we have already
sion of mobbing in black-
·d bats) in which imitation
y trained to exhibit one of
:rved by a naïve individual.
e behavior that its trained
· for a second naïve individ-
finitely (e.g., Dindo et al.,
haviors across cultural gen-
:hey, like humans, may be
the subject of the final sec-

possibility that animals are
·o repeat arbitrary actions

performed by a human demonstrator when the demonstrator says "Do this" and then presenting these trained subjects with new arbitrary actions to see if these are also copied when the human demonstrator says "Do this." Obviously, in order for the *do-this* experimental strategy to work, the animal subject has to be able to produce motor patterns similar to those produced by its human demonstrator. Consequently, such experiments have generally used monkeys or apes as subjects (for review, see Whiten & Custance, 1996), though an interesting exception, Moore's (1992) work with an African gray parrot, is also described below.

Using the do-this method Tomasello and colleagues (1993) studied imitation in two-year-old human infants and chimpanzees that had been raised either by humans or by their natural mothers. All subjects watched while a human demonstrated a series of novel actions directed toward objects. For example, subjects saw a human demonstrator place an object on her head or use a lever to pry open the lid of a paint can. The children were told, "Do this," and the apes had been previously trained to reproduce familiar actions when they saw a human engage in them. Apes reared by humans and two-year-old children imitated the experimenter's actions both frequently and equally often, whereas chimpanzees reared by members of their own species did not imitate the actions of their demonstrators (for review, see Whiten & Custance, 1996; Tomasello, 2009).

Some animals seem to imitate human actions even without explicit training. Bruce Moore (1992) housed an African gray parrot (*Psittacus erithacus*) that he named Okichoro alone in a room that contained, along with the usual perches and toys, a microphone and video camera that allowed Moore to observe Okichoro's behavior while she was undisturbed.

Moore visited with Okichoro several times each day for more than five years and during each visit repeatedly performed several distinct movements, accompanying each with a different spoken word or phrase. For example, Moore often said, "Look at my tongue!" and then stuck out his tongue. And each time Moore left, he waved good-bye and said, "Ciao!"

Okichoro rapidly learned to say "caio" and after a year was observed while alone in her room saying "ciao" and then waving her foot. A few months later Okichoro started saying "Look at my tongue," then opening her mouth and raising her tongue.

Over the years, the parrot spontaneously copied six different actions involving six different parts of her body while coupling each action with the appropriate word or phrase. Inappropriate pairings of words and actions were rare (for review, see Moore, 1996). The performance of Okichoro, like that of Alex (a fellow gray parrot), was so extraordinary that it has yet to be incorporated in general discussions of imitation in animals.

Anecdote—Much of the evidence consistent with the view that animals can imitate comes from serendipitous observations made outside the laboratory, suggesting that individual animals from chimpanzees (seen to open paint cans, sharpen pencils, and use sandpaper) to dolphins (reported to copy the behavior of a diver cleaning the windows on their aquarium) have learned complex patterns of behavior by imitating human caretakers' behavior (for review, see Moore, 1992).

Perhaps the most famous of the many anecdotal examples of animals imitating human behavior involved a cat that had learned to open a garden gate by jumping up and depressing the thumb piece of the gate latch with one forepaw while simultaneously pushing at the gate post with its hind legs. The observer of the cat's behavior concluded that the cat must have seen humans open the gate by depressing the latch and simultaneously pushing at the gate and reasoned, "If a hand can do it, why not a paw," then produced the required behavior (Romanes, 1884)—maybe, maybe not.

Although Romanes surely observed the behavior he described, there are at least two reasons to be cautious in attributing such behaviors to animals being able to learn to do acts from seeing others engage in them. First and most important, anecdotal observations in uncontrolled environments rarely provide insight into how improbable, human-like behaviors develop in animals. *Did the cat observe the gate being opened and then reproduce the behavior it had seen, or did the behavior of a caretaker focus the cat's attention on the gate latch and result in numerous contacts with the handle that eventually led to the cat learning to open the gate by trial and error?* It is impossible to tell from just watching the cat after it has learned the relevant actions.

Second, tens of millions of people watch tens of millions of pets for hours each day, but it is only in those rare instances when an animal appears to copy a behavior of its owner that the incident is reported to others. No one talks about the countless millions of times when pets see their owners engage in a potentially useful behavior without copying (Visalberghi & Fragaszy, 1990). Such selective reporting of positive instances cannot exclude chance correspondences between the behavior of an animal and that of humans with whom the animal interacts.

One approach to avoiding problems inherent in using chance observation of possibly interesting behaviors is to formalize the observation of behavior in uncontrolled environments. For example, Anne Russon and Birute Galdikas (1993) worked at a camp in Borneo where orangutans that had been captured by poachers and raised in captivity were reintroduced to life in the wild. The apes were free to come and go from the jungle to the camp, where they both interacted with the camp's human inhabitants and were provided with food while they made the transition to life in the wild.

he view that animals can imi-
:ide the laboratory, suggesting
·o open paint cans, sharpen
 copy the behavior of a diver
d complex patterns of behav-
:w, see Moore, 1992).

al examples of animals imi-
urned to open a garden gate
 the gate latch with one fore-
ost with its hind legs. The
cat must have seen humans
neously pushing at the gate
 paw," then produced the
rbe not.

or he described, there are at
ι behaviors to animals being
ge in them. First and most
d environments rarely pro-
haviors develop in animals.
·eproduce the behavior it had
·'s attention on the gate latch
hat eventually led to the cat
mpossible to tell from just
ctions.

of millions of pets for hours
a an animal appears to copy
ted to others. No one talks
ee their owners engage in a
lberghi & Fragaszy, 1990).
not exclude chance corre-
 and that of humans with

n using chance observation
he observation of behavior
Anne Russon and Birute
re orangutans that had been
: reintroduced to life in the
: jungle to the camp, where
abitants and were provided
ι the wild.

The behavior of the apes was systematically observed, and video recordings were made of dozens of behavior sequences in which the apes appeared to copy human behaviors. For example, a female orangutan unscrewed caps from two fuel drums, then inserted the end of a hose into one fuel drum, inserted the other end into her mouth, bellowed her cheeks, and after much fooling around with the end of the hose that had been in her mouth, placed it in the other fuel drum. Although the fuel drum the ape had selected to start her procedure was empty and the timing between sucking on one end of the hose and inserting it into the second rum was inappropriate, the sequence of acts was similar to that of a human siphoning fuel from one can to another, an act regularly carried out by camp staff.

As with the earlier field studies of imitation, although it is impossible to know just how the ape came to exhibit such a complex series of human-like behaviors, the numerous cases of potential imitation that Russon and Galdikas filmed suggest that, under some circumstances, orangutans can imitate. Perhaps most important, videotapes of the apparently imitative behaviors are available to those interested in viewing them so that others may make their own judgments concerning the apes' behavior. Some will surely be impressed by the similarity of the apes' performance to that of humans. Others may wonder at the apes' apparent lack of directedness as they move, often painfully slowly, through a behavior sequence. Indeed, some have argued that apes do not understand the goal of a demonstrator in the same way that humans do and consequently do not imitate with the same intentionality, instead simply reproducing behaviors without connecting those behaviors with their goal (Tomasello, 2009).

To the contrary, others have suggested that free-living animals learn complex patterns of behavior by imitation and that such imitation provides the foundation for purported behavioral traditions that have been observed in many species. However, important questions remain as to how such behaviors develop in the individuals and populations that exhibit them and the relationship of such patterns of behavior in animals to human culture. Both issues are discussed in the final sections of this chapter.

TRADITIONS AND CULTURE

Historical Examples of Animal Tradition: Japanese Macaques and British Birds

Japanese macaques—Perhaps the best-known instance of the possible spread of a complex behavior through a population of animals by imitation came from studies of a free-living (though provisioned) troop of Japanese macaques resident on Koshima Islet, a small island in the Sea of Japan (Kawai, 1965).

In 1953, an 18-month-old female macaque (Imo) began to take pieces of sweet potato left on a beach by a provisioner (and consequently covered with sand) to a stream and to wash the sand from the potato pieces before eating them.

Most Japanese macaques use their hands to brush any sand or dirt from pieces of sweet potato left for them. However, Imo started washing potato pieces in water, and the habit of sweet-potato washing gradually spread through her troop. First Imo's playmates and then Imo's mother learned the behavior, and over the next nine years 14 of 15 juveniles and 2 of 11 adults in Imo's troop started washing their sweet potatoes. This sweet-potato washing, as well as several other unusual behaviors seen in the Koshima troop (from eating fish to bathing in the ocean), have been interpreted in innumerable secondary sources as products of imitation, though those who first described them were considerably more cautious (Kawai, 1965).

Of course, we will never know with certainty what caused sweet-potato washing to spread through the Koshima troop more than 50 years ago. However, there are reasons to question the common interpretation of the behavior as spreading by imitation: (1) the behavior spread extremely slowly (Galef, 1992) with individuals taking, on average, more than two years each to acquire it; (2) the behavior of washing food is not so unlikely in macaques as intuition would suggest (Visalberghi & Fragaszy, 1990); and (3) provisioners may have inadvertently trained the monkeys to exhibit the behavior (Green, 1975).

British birds—In the years following World War II several species of titmice residing in Great Britain acquired the habit of opening milk bottles left on doorsteps by milk delivery services common at the time, pecking at the cardboard lids used to seal the bottles and then drinking cream from the surface of the milk (which was not homogenized). The original investigators of the geographic spread of the behavior were cautious in their interpretation of its causes. After all, simple local enhancement might suffice (Fisher & Hinde, 1949). However, as with the Koshima macaques's sweet-potato washing, textbooks frequently attributed the spread of milk-bottle opening to learning by imitation. More recent, controlled experiments with chickadees, North American birds closely related to the British titmice, have shown that simply drinking cream from milk bottles opened by others can induce birds to start pecking at closed milk bottles and opening them for themselves (Sherry & Galef, 1984).

Obviously, we have some way to go before we understand the development of unusual behaviors in free-living populations and the role, if any, of social learning in producing such differences. The use of tools to capture insects by woodpecker finches in the Galápagos Islands and crows in New Caledonia

no) began to take pieces of
d consequently covered with
: potato pieces before eating

ɔrush any sand or dirt from
Imo started washing potato
ɔ washing gradually spread
ɛn Imo's mother learned the
juveniles and 2 of 11 adults
ɔes. This sweet-potato wash-
ι in the Koshima troop (from
erpreted in innumerable sec-
h those who first described
965).

y what caused sweet-potato
ɔre than 50 years ago. How-
ιterpretation of the behavior
ad extremely slowly (Galef,
ιan two years each to acquire
ɕely in macaques as intuition
ιd (3) provisioners may have
behavior (Green, 1975).

ιr II several species of titmice
ɔpening milk bottles left on
ιe time, pecking at the card-
ɕing cream from the surface
original investigators of the
in their interpretation of its
ht suffice (Fisher & Hinde,
ɛ sweet-potato washing, text-
ottle opening to learning by
ts with chickadees, North
ιce, have shown that simply
ers can induce birds to start
n for themselves (Sherry &

understand the development
nd the role, if any, of social
ɔf tools to capture insects by
ιd crows in New Caledonia

provide further examples of problems encountered in determining the role of social learning in development of complex behaviors.

More Recent Examples of Animal Tradition in Birds

Galápagos finches—Galápagos woodpecker finches (*Camarhynchus pallidus*) are famous for their use of twigs and cactus spines as tools to pry arthropods out of crevices in the bark of trees. If such a complex pattern of behavior were to be observed in a cetacean or primate, it would surely be viewed as a possible tradition resting on imitative learning. However, when Sabine Tebbich and colleagues (2001) examined the development of tool use by woodpecker finches, they found no evidence that social learning played any role at all.

Juvenile woodpecker finches used tools to look for prey even if they had never seen tool use demonstrated by others, and adults that had been captured in damp areas, where tool use is rarely seen, never learned to use tools either by trial and error or after observation of conspecifics demonstrating the technique. Tebbich and colleagues (2001) interpreted their findings as indicating that Galapagos woodpecker finches are predisposed to learn to use tools by trial and error, but only during a sensitive period early in development.

New Caledonian crow—In nature, New Caledonian crows (*Corvus moneduloides*) (relatives of North American crows) manufacture tools from leaves and use these tools to retrieve food hidden in crevices, much as woodpecker finches in the Galapagos use twigs for the same purpose. Differences in the types of tool and number of types of tool found in different locations on New Caledonia suggest that there may be traditions of tool use in crow populations (for review, see Holzhaider et al., 2010).

Ben Kenward and colleagues (Kenward et al., 2006) hand-reared four New Caledonian crows in captivity, giving the maturing birds no opportunity to interact with tool-using adults of their species. All four hand-reared birds developed the ability to use twig tools, and one of them both cut a simple tool from a leaf and used it to obtain hidden food. Observation of a human demonstrator handling potential tools increased the attention that hand-reared young crows paid to the tools they saw handled but had no influence on their tool manufacture or use (Kenward et al., 2006).

The general message in examples such as cats opening garden gates, monkeys washing sweet potatoes, and birds opening milk bottles and using tools to get insects out of crevices is that, although discovery of unusual behavior in an individual or population is suggestive and interesting, such discovery tells us nothing definitive about the processes responsible for the development of a behavior in the individuals and populations exhibiting it. In some cases,

analyses under controlled conditions of instances of apparent tradition in free-living animals have raised questions about the validity of explanation in terms of social learning. In other cases, controlled studies have strengthened interpretation of an unusual behavior as dependent on social learning.

Evidence of Tradition and Culture in Apes: The Method of Exclusion

Discovery of multiple differences in the behavioral repertoires of various troops of free-living chimpanzees and orangutans has led to the controversial proposal that they, like humans, are bearers of culture. Part of the controversy over ape culture reflects disagreement as to how culture should be defined. However, all involved in such controversy are agreed that, at a very minimum, for observed differences in the behavioral repertoires of diverse groups of apes to be considered as even potentially cultural, such differences have to be a result of social learning (for review, see Laland & Galef, 2009).

In 1999, Andy Whiten, at St. Andrews University in Scotland, and numerous collaborators, who together had accumulated more than 150 person-years of observation of seven geographically distinct populations of chimpanzees in their home environments in East and West Africa, presented evidence that each chimpanzee population exhibits a unique behavioral repertoire in food-processing techniques and social customs (Whiten et al., 1999). Indeed, description of the behavioral repertoire of a population is sufficient to identify that population, much as one could identify human populations as, say, North American or Asian on the basis of description of their social customs and methods of processing food. Carel van Schaik and collaborators (van Schaik et al., 2003) have provided a similar analysis of variation in the behavioral repertoires of populations of orangutans in Indonesia. Because the issues are similar and the data from chimpanzees is more elaborated than that for orangutans, I focus here solely on the question of whether chimpanzees have been shown to exhibit culture.

Whiten and his coauthors used what they called the *method of exclusion* to attribute to social learning the distribution of 39 behaviors that are customary (i.e., all relevant individuals show the behavior) or habitual (i.e., several individuals show the behavior) in some of the seven chimpanzee communities they examined but absent in others. The label "method of exclusion" refers to the fact that attribution of a behavior to social learning depended upon exclusion of alternative explanations of interpopulation differences in behavior, for example, differences in the genetic makeup of communities or differences in behavior in response to differences in the environments that different populations inhabit.

of apparent tradition in free-
idity of explanation in terms
lies have strengthened inter-
1 social learning.

)n

ivioral repertoires of various
s has led to the controversial
lture. Part of the controversy
/ culture should be defined.
eed that, at a very minimum,
ires of diverse groups of apes
ich differences have to be a
: Galef, 2009).
sity in Scotland, and numer-
more than 150 person-years
ipulations of chimpanzees in
ica, presented evidence that
ehavioral repertoire in food-
iiten et al., 1999). Indeed,
lation is sufficient to identify
in populations as, say, North
of their social customs and
id collaborators (van Schaik
riation in the behavioral rep-
i. Because the issues are sim-
: elaborated than that for
f whether chimpanzees have

d the *method of exclusion* to
behaviors that are customary
ir habitual (i.e., several indi-
n chimpanzee communities
method of exclusion" refers
ial learning depended upon
ilation differences in behav-
ip of communities or differ-
in the environments that

Ecological Effects on "Traditional" Behaviors of Chimpanzees

Perhaps the most carefully studied of the 39 possibly cultural behaviors described by Whiten and his collaborators concerns chimpanzees' use of tools to capture and eat army ants. At Gombe, in Tanzania in East Africa, chimpanzees "dipping" for ants hold a long branch that they have stripped of leaves in one hand, introduce the distal end of the branch into a nest of army ants, and then quickly withdraw the branch as the ants charge up it to attack. The chimpanzee then sweeps the length of the wand with its free hand, collecting the ants into a loose ball, which it then pops into its mouth.

In the Tai Forest in the Ivory Coast in West Africa, ant-dipping chimpanzees use a short stick to collect a relatively small number of ants and strip the ants from the stick by directly pulling the stick through their mouths. The Tai technique, using the short stick, results in a significantly lower rate of ant capture than the long-stick technique seen at Gombe.

Chimpanzees at Bossou, in Guinea in West Africa, use both the Tai and Gombe techniques but use the apparently less efficient short-stick-directly-into-the-mouth technique considerably more frequently than they use the apparently more efficient long-stick-hand-to-mouth technique. Chimpanzees in the Budungo forest in Uganda (East Africa) do not feed on army ants even though there are plenty of army ants present there for chimps to feed on. In accord with the cultural hypothesis, simple description of whether and how ants are exploited suffices to identify four chimpanzee communities.

A second widely studied, purportedly traditional behavior involves the methods used by some chimpanzees to crack open hard nuts to gain access to their nutritious kernels. For example, most chimpanzee populations to the west of the N'Zo-Sassandra River in the Ivory Coast use stone hammers and anvils to crack open nuts, whereas those to the east of the river, which forms a barrier to gene flow between populations, rarely do so. The distribution of nut-cracking behavior could not be explained by differences in the density of chimpanzees, the density of nut-bearing trees, or the frequency with which objects suitable for use as hammers and anvils are encountered to the east and west of the river.

Although between-population variation in such complex and apparently socially learned behaviors as *ant dipping* and nut cracking provides evidence consistent with the assertion that, like their human cousins, chimpanzees are bearers of culture, that assertion has not been universally accepted. There are two general reasons for such challenges; the first involves a fundamental problem with the method of exclusion itself.

Because it is always possible that some as yet undiscovered ecological or genetic difference between communities may explain any observed difference in their behavior, conclusively demonstrating by the method of exclusion that

behavioral divergence between two populations results from social learning is logically impossible (Laland & Janik, 2006). Indeed, there is evidence that such exclusion may be more difficult than it seems.

Ant dipping—Tatyana Humle and Tetsuro Matsuzawa (2002) investigated the role of nonsocial factors in chimpanzees' use of long and short sticks when dipping for army ants. They found that the aggressiveness of the ant species being preyed upon by chimpanzees predicted which of the two techniques chimpanzees at Bossou use when dipping for ants. To feed on aggressive black ants, chimpanzees use a long wand and their hand to remove ants from the probe, whereas chimpanzees feeding on less-aggressive red ants use a short stick and their mouths to remove ants directly from the stick.

A simple experiment in which humans used wands of different lengths to dip into nests of red and black ants revealed that the black ants swarmed up the probes in greater numbers and delivered far more painful bites than did the red ants. Consequently, it is not too surprising that chimpanzees used long probes when dealing with the more aggressive and harmful black ants than when dealing with relatively benign red ants and collected more ants per unit time when feeding on the former than the latter.

Of course, the finding at Bossou that the method used to dip for ants is affected by prey behavior does not mean that the different ant-dipping techniques used by chimpanzees at Tai and Gombe are also responses to differences in prey behavior at the two sites. In fact, a comparison of the behavior of chimpanzees at Bossou and at Tai (where only the short-stick technique is seen) revealed that although both aggressive and nonaggressive ants are present at Tai, Tai chimps feed only on the less aggressive red ants (Mobius et al., 2008). Thus, social custom determining which ants are eaten at Tai and Bossou might be indirectly responsible for the difference in feeding techniques seen at the two locations. Alternatively, some as yet undescribed ecological factor might determine the kinds of ants that chimpanzees choose as prey. If so, the methods chimpanzees use to prey on ants might not be traditional at all.

Genetic Effects on Traditional Behaviors of Chimpanzees

Recent research has also provided evidence of a strong statistical correlation between the genetic distance between chimpanzee populations (determined by number of nucleotide differences) and the extent of their behavioral diversity (Langergraber et al., 2011). However, even such strong correlations between genetic distance and behavioral dissimilarity cannot be interpreted uncritically as showing that social transmission processes are less important than previously believed in producing observed differences in behavior patterns. High rates of short-distance migration between chimpanzee communities of females

ns results from social learning is
. Indeed, there is evidence that
eems.
Matsuzawa (2002) investigated
se of long and short sticks when
iggressiveness of the ant species
d which of the two techniques
nts. To feed on aggressive black
hand to remove ants from the
·aggressive red ants use a short
' from the stick.
·d wands of different lengths to
:hat the black ants swarmed up
far more painful bites than did
;ing that chimpanzees used long
·e and harmful black ants than
nd collected more ants per unit
er.
method used to dip for ants is
the different ant-dipping tech-
be are also responses to differ-
, a comparison of the behavior
nly the short-stick technique is
l nonaggressive ants are present
essive red ants (Mobius et al.,
iich ants are eaten at Tai and
lifference in feeding techniques
yet undescribed ecological fac-
npanzees choose as prey. If so,
night not be traditional at all.

·f a strong statistical correlation
:ee populations (determined by
nt of their behavioral diversity
:h strong correlations between
mot be interpreted uncritically
are less important than previ-
:es in behavior patterns. High
)anzee communities of females

carrying the behavioral variants of their natal troops could result in a positive correlation between genetic and behavioral distance, even if behavioral variants were entirely socially learned. At the time of this writing, interpretation of Langergraber and colleagues' (2011) data remains controversial.

Possible Resolution

Evidence appears to be gradually accumulating indicating that behavioral differences among chimpanzee populations are likely to result from the combined action of genetic, ecological, and social factors. As Kevin Laland and Vincent Janik (2006, p. 545) have proposed, "Researchers studying animal culture would be better advised to think in terms of partitioning variance to alternative sources. The prime issue in the animal culture debate is not whether a given behavior is learned socially or asocially, but rather how much of the variance in the behavior can be attributed to social learning." Some field researchers seem to agree (Mobius et al., 2008), and a resolution of the "culture wars," similar to that which defused the controversy regarding the role of genes and environment in development of the behavior of individuals, seems possible. In the final analysis, the cultural hypothesis of the origins of behavioral diversity among chimpanzee populations is a hypothesis concerning the development of relevant behaviors. Consequently, anticipating parallel resolutions of the "nature-nurture controversy" and the culture wars is reasonable (see Chapter 5 in this volume).

Development of Traditional Behaviors of Chimpanzees

Termite fishing—The cultural hypothesis asserts, almost invariably in the absence of direct evidence, that social interactions among group members are the source of the behaviors present in some populations but absent in others. For example, following a four-year field study of development of *termite fishing* (a tool-using behavior akin to ant dipping) in young chimpanzees, Elizabeth Lonsdorf (2006) found that there is substantial variation in both the time females spend termite fishing in the presence of their young and the ages at which their offspring become proficient fishers of termites. However, proficiency was best predicted not by variation in the time mothers spend termite fishing in the presence of their offspring but by the gender of the young, clearly a genetic factor.

Young of both sexes appear to learn from their mother both that the termite mound is an object to which attention should be directed and that the goal of activity at the mound is to capture termites. Male offspring subsequently develop their own fishing technique without much reference to the details of

their mothers' behavior while young females seem to learn something of the proper form of the behavior from watching their mothers. In particular, daughters, but not sons, insert probes to the same depth into termite nests as did their mothers. Young of both sexes then had to learn by trial and error how to withdraw a tool from the nest without knocking off termites (Lonsdorf et al., 2004). Social interaction, genetic predisposition, and trial-and-error learning each seem to play some role in development of termite fishing, although the extent of social influence on development of the behavior was not great.

Nut cracking—Observations of interactions of adult and young chimpanzees at nut-cracking sites, like observation of young at termite mounds, are only partly consistent with the view that nut cracking is socially learned. Adults frequently chase away juveniles trying to take nuts and stones, and rearing by a mother who did not engage in nut cracking did not slow acquisition of nut cracking by her offspring (Inoue-Nakamura & Matsuzawa, 1997). Indeed, Noriko Inoue-Nakamura and Matsuzawa (1997, p. 172) conclude that "the members of a community provided the infants only with the opportunity to freely access nuts and stones. These opportunities could facilitate the individual experience of stone-nut manipulation and result in the apparent social transmission of tool use behavior among the wild chimpanzees." Providing infants with the opportunity to freely access nuts and stones, a form of local enhancement, can provide the basis for a tradition in a population. However, as discussed in the next section, the distinction between such social enhancement of behavior and learning directly by imitation or teaching may be important in understanding the differences between animal and human culture.

Concluding Remarks on the Method of Exclusion

The point of the present section is not that social learning plays little role in development of the 39 potential cultural behaviors identified by Whiten and colleagues (1999). Rather, it seems reasonable to conclude that knowledge of the development of purportedly traditional behaviors is currently insufficient to determine either which of the 39 behaviors identified by Whiten and colleagues (1999) as cultural are influenced in their development by social learning or the kind of social learning involved in development of those behaviors that are socially influenced.

"Culture" in Chimpanzees and Humans: Analogy or Homology?

There is considerable diversity in views regarding the relationship between the culture of humans and of other animals (Laland & Galef, 2009). Some

em to learn something of the
mothers. In particular, daugh-
h into termite nests as did their
by trial and error how to with-
off termites (Lonsdorf et al.,
n, and trial-and-error learning
? termite fishing, although the
e behavior was not great.
of adult and young chimpan-
young at termite mounds, are
: cracking is socially learned.
take nuts and stones, and rear-
·cking did not slow acquisition
amura & Matsuzawa, 1997).
awa (1997, p. 172) conclude
e infants only with the oppor-
portunities could facilitate the
on and result in the apparent
he wild chimpanzees." Provid-
ss nuts and stones, a form of
adition in a population. How-
tinction between such social
by imitation or teaching may
s between animal and human

cial learning plays little role in
iors identified by Whiten and
to conclude that knowledge of
aviors is currently insufficient
identified by Whiten and col-
r development by social learn-
evelopment of those behaviors

rding the relationship between
Laland & Galef, 2009). Some

see no reason to make a distinction, whereas others prefer to restrict use of the term *culture* to our own species. All agree that both animal traditions and human culture function similarly, both providing naïve individuals with access to innovative adaptive behaviors that others of their species have developed and reducing potential costs to naïve individuals of acquiring adaptive behaviors. However, some argue that human culture serves additional functions never seen in animal traditions (for example, use of arbitrary social conventions, such as hairstyle or facial decoration, to define group identity [Perry, 2009] or regulation of individual behavior by enforced adherence to specific systems of rules [Hill, 2009]). Others are less concerned with differences in function than with differences in both the processes producing traditions in animals and humans and the nature of the products of those processes (Galef, 2009; Hill, 2009; Tomasello, 2009).

Human culture, particularly human material culture, cumulates over generations, and as a result can produce increasingly complex and sophisticated artifacts and patterns of behavior (Boyd & Richerson, 1996; Tomasello, 2009). A scant handful of chimpanzee behaviors have been interpreted as providing possible instances of cumulative culture (for review, see Whiten et al., 2003). However, each such example is open to alternative, simpler interpretations, and no one has claimed that any ape has learned any behavior socially that it could not learn for itself from interacting with its asocial environment.

Much of the behavior in which humans engage is, to the contrary, clearly a product not of individual learning but of knowledge accumulated across cultural generations. This *ratcheting* (Tomasello, 1990), seen in all human populations, depends upon a naïve observer being able to acquire a close copy of the behavior of a proficient demonstrator. Only a precise copy can serve as a base (or scaffold) for subsequent modifications, allowing an iterative process in which each new modification becomes a scaffold for further modification, in turn allowing the emergence of gradually increasing complexity in behavior.

Existence of ratcheting in human traditions and its absence in animal traditions suggests a fundamental difference in the developmental processes supporting animal traditions and human culture (Galef, 1992). For example, György Gergely and Gergely Csibra (2006) have provided experimental evidence that children will copy the behavior of a model with greater fidelity when provided with explicit pedagogical cues and suggest that such *guided transmission* is essential to the faithful social learning of complex skills. Lauraeno Castro and Miguel Toro (2004) suggest that both increased efficiency in imitation and development of a capacity to approve or disapprove of the learned behavior of others (a simple form of teaching) were necessary for the emergence of cumulative culture. In either case, uniquely human processes, particularly

teaching and precise imitation (which, like teaching, can at least in principle result in precise copying of behavior), are seen as providing a necessary substrate for cumulative culture. Current evidence suggests that chimpanzees never teach, are not as proficient imitators as are humans (Whiten, 2005), and have no symbolic language (unless taught one by humans) with which to instruct others.

Much of animal social learning depends on local enhancement or emulation. As a result of either, a naïve individual has to develop for itself the behaviors that it directs towards portions of the environment to which the behavior of others has directed its attention. In local enhancement and emulation, there is no precise copying of behavior and consequently no possibility of cumulative improvement in performance over behavioral generations.

The extent to which members of traditional human societies engage in teaching has been controversial (e.g., Whiten et al., 1980; Laland & Hoppitt, 2003), possibly because of undue focus in the ethnographic literature on explicit linguistic instruction. Such focus tended to overlook nonverbal behaviors of potential teachers that facilitating acquisition by their pupils. A recent review of the archaeological and ethnographic evidence of teaching that adopts a definition of teaching similar to that employed by students of animal behavior (Caro & Hauser, 1992) suggests "the gradual scaffolding of skills in a novice through demonstration, intervention and collaboration ... has played an essential role in securing the faithful transmission of skills across generations and should be regarded as the central mechanism through which long-term and stable material culture traditions are propagated and maintained" (Tehrani & Riede, 2008, p. 316).

CONCLUSION

Perhaps in time we shall discover that apparent differences between the products of social learning in humans and animals are trivial rather than profound and that small differences in capacity have resulted in huge differences in performance. Until then, we need to explore both differences and similarities in the behavioral substrate(s) of human and animal "culture."

Laland (2004) has suggested that an ability to evaluate the relative utility of behavioral alternatives may be a cognitive requirement for the emergence of human-like cumulative culture. Tomasello (1999) has proposed that imitation and teaching, which he sees as critical to establishment of cumulative culture, require a capacity to take the perspective of a model or pupil, a capacity that—like that for culture—is far more fully developed in humans than in other species. Gergely and Csibra (2006) suggest that human cultural capacities coevolved with the ability to learn and transfer knowledge through teaching,

ching, can at least in principle
 providing a necessary substrate
s that chimpanzees never teach,
hiten, 2005), and have no sym-
rith which to instruct others.

n local enhancement or emu-
il has to develop for itself the
he environment to which the
i local enhancement and emu-
.nd consequently no possibility
er behavioral generations.

ial human societies engage in
t al., 1980; Laland & Hoppitt,
ie ethnographic literature on
l to overlook nonverbal behav-
sition by their pupils. A recent
vidence of teaching that adopts
d by students of animal behav-
al scaffolding of skills in a nov-
:ollaboration ... has played an
ion of skills across generations
ism through which long-term
iropagated and maintained"

arent differences between the
nals are trivial rather than pro-
.ve resulted in huge differences
e both differences and similar-
.d animal "culture."

o evaluate the relative utility of
iirement for the emergence of
)9) has proposed that imitation
ishment of cumulative culture,
odel or pupil, a capacity that—
d in humans than in other spe-
at human cultural capacities
: knowledge through teaching,

which they suggest is a process independent from, and possibly antecedent to, either language or the ability to attribute mental states. Vaesen (2011) has discussed eight cognitive abilities of humans but lacking in apes that make cumulative culture difficult, if not impossible, for apes to achieve.

It is, of course, far easier to generate than to test hypotheses concerning the necessary cognitive substrate of cumulative culture. However, if any such suggestions are correct, culture of the human kind may well have arisen only in the ancestral hominid line after its divergence from that of the great apes some 6 or 7 million years ago. If so, despite the close phylogenetic relationship between *Homo sapiens* and other extant great apes, the traditions of animals may provide little insight into the evolution of the human capacity for cumulative culture.

ACKNOWLEDGMENTS

REFERENCES AND SUGGESTED READING

Bateson, P. P. G. & P. Martin. (1999). *Design for a Life: How Behavior Develops*. London: Jonathan Cape.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, 41, 530–532.

Boyd, R. & P. J. Richerson. (1996). Why culture is common but cultural evolution is rare. *Proceedings of the British Academy*, 88, 77–93.

Campbell, F. M., C. M. Heyes, & A. R. Goldsmith. (1999). Stimulus learning and response learning by observation in a two-object/two-action test. *Animal Behaviour*, 58, 151–158.

Caro, T. M. & M. D. Hauser. (1992). Is there teaching in non-human animals? *Quarterly Review of Biology*, 67, 151–174.

Castro, L. & M. A. Toro. (2004). The evolution of culture: From primate learning to human culture. *Proceedings of the National Academy of Sciences, USA*, 101, 10235–10240.

Cornell, H. N., J. M. Marzluff, & S. Pecoraro. (2011). Social learning spreads knowledge about dangerous humans among American crows. *Proceedings of the Royal Society of London, B*, 279, 499–508.

Curio, E. (1988). Cultural transmission of enemy recognition by blackbirds. In T. R. Zentall & B. G. Galef, Jr. (eds.), *Social Learning: Biological & Psychological Perspectives* (pp. 75–98). Hillsdale, NJ: Lawrence Erlbaum Associates.

Dawson, B. V. & B. M. Foss. (1965). Observational learning in budgerigars. *Animal Behaviour*, 13, 470–474.

Diamond, J. (2001). Unwritten knowledge. *Nature*, 410, 521.

Dindo, M., B. Thierry, & A. Whiten. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society of London, B*, 275, 187–193.

Dugatkin, L. (1996). Copying and mate choice. In C. M. Heyes & B. G. Galef, Jr. (eds.), *Social Learning in Animals: The Roots of Culture* (pp. 85–106). San Diego, CA: Academic Press.

Fisher, J. & R. A. Hinde. (1949). The opening of milk bottles by birds. *British Birds*, 42, 347–357.

Forsman, J. T. & R. L. Thomson. (2008). Evidence of information collection from heterospecifics in cavity-nesting birds. *Ibis*, 150, 409–412.

Fragaszy, D. M. & S. Perry. (2003). *The Biology of Traditions*. Cambridge, UK: Cambridge University Press.

Franks, N. R. & T. Richardson. (2006). Teaching in tandem-running ants. *Nature*, 439, 153.

Freeberg, T. M. (2004). Social transmission of courtship behavior and mate preference in brown-headed cowbirds, *Molothrus ater*. *Learning & Behavior*, 32, 122–130.

Galef, B. G., Jr. (1977). Mechanisms for the transmission of acquired food preferences from adult to weanling rats. In L. M. Barker, M. R. Best, & M. Domjan (eds.), *Learning Mechanisms in Food Selection* (pp. 123–150). Waco, TX: Baylor University Press.

Galef, B. G., Jr. (1981). The development of olfactory control of feeding site selection in rat pups. *Journal of Comparative and Physiological Psychology*, 95, 615–622.

Galef, B. G., Jr. (1985). Social learning in wild Norway rats. In T. D. Johnston & A. T. Pietrewicz (eds.), *Issues in the Ecological Study of Learning* (pp. 143–166). Hillsdale, NJ: Lawrence Erlbaum Associates.

Galef, B. G., Jr. (1988). Communication of information concerning distant diets in a social, central-place foraging species: *Rattus norvegicus*. In T. R. Zentall & B. G. Galef Jr. (eds.), *Social Learning: Biological & Psychological Perspectives* (pp.119–139). Hillsdale, NJ: Lawrence Erlbaum Associates.

Galef, B. G., Jr. (1992). The question of animal culture. *Human Nature*, 3, 157–178.

Galef, B. G., Jr. (1996). Social enhancement of food preferences in Norway rats: A brief review. In C. M. Heyes & B. G. Galef Jr. (eds.), *Social Learning and Imitation: The Roots of Culture* (pp. 49–64). New York: Academic Press.

Galef, B. G. (2009). Culture in animals? In K. N. Laland & B. G. Galef Jr. (eds.), *The Question of Animal Culture* (pp. 222–246). Cambridge, MA: Harvard University Press.

:ognition by blackbirds. In T. R.
ng: *Biological & Psychological Per-*
Erlbaum Associates.
learning in budgerigars. *Animal*

410, 521.
:ial diffusion of novel foraging
apella). Proceedings of the Royal

C. M. Heyes & B. G. Galef, Jr.
s of Culture (pp. 85–106). San

lk bottles by birds. *British Birds,*

: of information collection from
0, 409–412.
of Traditions. Cambridge, UK:

n tandem-running ants. *Nature,*

tship behavior and mate prefer-
ater. Learning & Behavior, 32,

nission of acquired food prefer-
rker, M. R. Best, & M. Domjan
on (pp. 123–150). Waco, TX:

y control of feeding site selection
logical Psychology, 95, 615–622.
ray rats. In T. D. Johnston & A.
udy of Learning (pp. 143–166).

ion concerning distant diets in a
orvegicus. In T. R. Zentall & B.
cal & Psychological Perspectives
im Associates.
ire. *Human Nature,* 3, 157–178.
d preferences in Norway rats: A
. (eds.), *Social Learning and Imi-*
York: Academic Press.
and & B. G. Galef Jr. (eds.), *The*
imbridge, MA: Harvard Univer-

Galef, B. G., Jr. & L. L. Buckley. (1996). Use of foraging trails by Norway rats. *Animal Behaviour, 51,* 765–771.

Galef, B. G., Jr. & M. M. Clark. (1971a). Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *Journal of Comparative and Physiological Psychology, 75,* 341–357.

Galef, B. G., Jr. & M. M. Clark. (1971b). Parent-offspring interaction determine time and place of first ingestion of solid food by wild rat pups. *Psychonomic Science, 25,* 15–16.

Galef, B. G., Jr. & L.-A. Giraldeau. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61,* 3–15.

Galef, B. G., Jr. & C. M. Heyes. (2004). Social learning & imitation. *Learning and Behavior, 32,* 1–140.

Garcia, J. & R. A. Koelling. (1966). The relation of cue to consequence in avoidance learning. *Psychonomic Science, 5,* 123–124.

Gergely, G. & G. Csibra. (2006). Sylvia's recipe: The role of imitation and pedagogy in the transmission of human culture. In N. J. Enfield & S. C. Levinson (eds.), *Roots of Human Sociality: Culture, Cognition and Human Interaction* (pp. 229–255). Oxford, UK: Berg.

Gibson, R. M., J. W. Bradbury, & S. L. Vehrencamp. (1991). Mate choice in lekking sage grouse revisited: the rolws of vocal display, female site fidelity, and copying. *Behavioral Ecology, 2,* 165–180.

Green, S. (1975). Dialects in Japanese Monkeys: vocal learning and cultural transmission of locale-specific vocal behavior? *Zeitschrift für Tierpsychologie, 38,* 304–314.

Griffin, A. S. (2004). Social learning about predators. *Learning & Behavior, 32,* 131–140.

Hepper, P. G. (1988). Adaptive fetal learning: prenatal exposure to garlic affects postnatal preference. *Animal Behaviour, 36,* 935–936.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46,* 999–1010.

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society, 69,* 207–231.

Heyes, C. M. (2012). What's social about social learning? *Journal of Comparative Psychology, 126,* 193–202.

Heyes, C. M. & B. G. Galef, Jr. (1996). *Social Learning in Animals: The Roots of Culture.* San Diego, CA: Academic Press.

Hill, K. (2009). Animal "culture"? In K. N. Laland & B. G. Galef Jr. (eds.), *The Question of Animal Culture* (pp. 269–287). Cambridge, MA: Harvard University Press.

Holzhaider, J. C., G. R. Hunt, & R. D. Gray. (2010). Social learning in New Caladonian crows. *Learning & Behavior, 38,* 206–219.

Hoppitt, W. J. E., G. R. Brown, R. Kendal, L. Rendell, A. Thornton, M. M. Webster, et al. (2008). Lessons from animal teaching. *Trends in Ecology and Evolution, 23,* 486–493.

Horner, V., A. Whiten, E. Flynn, & F. B. M. de Waal. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences, USA, 103,* 1378–1383.

Humle, T. & T. Matsuzawa. (2002). Ant dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology, 58,* 133–148.

Inoue-Nakamura, N. & T. Matsuzawa. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 111,* 159–173.

Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates, 6,* 1–30.

Kendal, R. L., B. G. Galef, & C. P. van Schaik. (2010). Social learning research outside the laboratory: How and why. *Learning and Behavior, 38,* 187–386.

Kenward, B., C. Rutz, A. A. S. Weir, & A. Kacelnik. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour, 72,* 1329–1343.

Laland, K. (2004). Social learning strategies. *Learning and Behavior, 32,* 4–14.

Laland, K. N. & B. G. Galef. (2009). *The Question of Animal Culture.* Cambridge, MA: Harvard University Press.

Laland, K. N. & W. Hoppitt. (2003). Do animals have culture? *Evolutionary Anthropology, 12,* 150–159.

Laland, K. N. & V. Janik. (2006). The animal culture debate. *Trends in Ecology and Evolution, 21,* 542–547.

Laland, K. N. & H. C. Plotkin. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning & Behavior, 18,* 246–251.

Langergraber, K. E., C. Boesche, M. Inoue-Muryama, J. Mitani, T. Nishida, A. Pusey, V. Reynolds, G. Schubert, R. W. Wrangham, E. Wroblewski, & L. Vigilant. (2011). Genetic and "cultural" similarity in wild chimpanzees. *Proceedings of the Royal Society of London, B, 278,* 408–416.

Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees? *Animal Cognition, 9,* 36–46.

Lonsdorf, E. V., A. E. Pusey, & L. Eberly. (2004). Sex differences in learning in chimpanzees. *Nature, 428,* 715–716.

Mineka, S. & M. Cook. (1988). Social learning and the acquisition of snake fear in monkeys. In T. R. Zentall & B. G. Galef, Jr. (eds.), *Social Learning: Biological & Psychological Perspectives* (pp. 99–116). Hillsdale, NJ: Lawrence Erlbaum Associates.

Mobius, Y., C. Boesch, K. Koops, T. Matsuzawa, & T. Humle. (2008). Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Animal Behaviour, 76,* 37–45.

Moore, B. R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour, 122,* 231–263.

aal. (2006). Faithful replication of
ssion chains by chimpanzees and
cademy of Sciences, USA, 103,

mong the chimpanzees of Bossou,
ites. *American Journal of Primatol-*

)evelopment of stone tool use by
! of Comparative Psychology, 111,

behavior of the natural troop of
es, 6, 1–30.
)10). Social learning research out-
and Behavior, 38, 187–386.
. (2006). Development of tool use
a patterns and social influences.

ng and Behavior, 32, 4–14.
n of Animal Culture. Cambridge,

lals have culture? *Evolutionary*

ure debate. *Trends in Ecology and*

ng and social transmission of for-
norvegicus). Animal Learning &

rama, J. Mitani, T. Nishida, A.
'rangham, E. Wroblewski, & L.
ilarity in wild chimpanzees. *Pro-*
, 408–416.

the acquisition of termite-fishing
ition, 9, 36–46.
:x differences in learning in chim-

d the acquisition of snake fear in
(eds.), *Social Learning: Biological*
illsdale, NJ: Lawrence Erlbaum

& T. Humle. (2008). Cultural
frican chimpanzees? A compara-
l Behaviour, 76, 37–45.
l a new form of mimicry: Tracing
Behaviour, 122, 231–263.

Moore, B. R. (1996). The evolution of imitative action. In C. M. Heyes & B. G. Galef, Jr. (eds.). *Social Learning in Animals: The Roots of Culture* (pp. 245–266). San Diego, CA: Academic Press.

Munger, S. D., T. Leinders-Zufall, L. M. McDougall, R. E Cockerham, A. Schmid, P. Wandernoth, G. Wennemuth, M. Biel, F. Zufall, & K. R. Kelliher. (2010). An olfactory subsystem that detects carbon disulfide and mediates food-related social learning. *Current Biology*, 20, 1438–1444.

Nielsen, M., F. Subiaul, A. Whiten, B. G. Galef, & R. R. Zentall. (2012). Social learning in humans and non-human animals: theoretical and empirical dissections. *Journal of Comparative Psychology*, 126, 109–113.

Page, R. A. & M. J. Ryan. (2006). Social transmission of novel foraging behavior in bats: Frog calls and their referents. *Current Biology*, 16, 1201–1205.

Perry, S. (2009). Are nonhuman primates likely to exhibit cultural capacities like those of humans? In K. N. Laland & B. G. Galef (eds.), *The Question of Animal Culture* (pp. 247–268). Cambridge, MA: Harvard University Press.

Ratcliffe, J. M. & H. M. ter Hofstede. (2005). Roosts as information centres: Social learning of food preferences in bats. *Biology Letters*, 1, 72–74.

Rendell, L. & H. Whitehead. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, 24, 309–324.

Romanes, G. J. (1884). *Mental Evolution in Animals*. New York: AMS Press.

Ruddle, K. & R. Chesterfield. (1997). Education for traditional food procurement in the Orinoco delta. *Ibero-American No. 53*. Berkeley, CA: University of California Press.

Russon, A. E. & B. M. F. Galdikas. (1993). Imitation in free-ranging rehabilitant orang-utans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 107, 147–161.

Seppanen, J.-T. & J. T. Forsman. (2007). Interspecific social learning: novel preference can be acquired from a competing species. *Current Biology*, 17, 1248–1252.

Sherry, D. F. & B. G. Galef Jr. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour*, 32, 937–938.

Smotherman, W. P. (1982). Odor aversion learning by rat fetus. *Physiology & Behavior*, 29, 769–771.

Steiniger, von F. (1950). Beitrage zur Soziologie une sonstigen Biologie der Wanderratte. *Zeitschrift für Tierpsycholgie*, 7, 356–379.

Stoinski, T. S., L. A. Drayton, & E. E. Price. (2011). Evidence of social learning in black-and-white ruffed lemurs (*Varecia variegata*). *Biology Letters*, 7, 376–379.

Tebbich, S., M. Taborsky, B. Fessl, & D. Blumqvist. (2001). Do wood-pecker finches acquire tool use by social learning? *Proceedings of the Royal Society of London, B*, 268, 2189–2193.

Tehrani, J. J. & F. Riede. (2008). Towards an archaeology of pedagogy: Learning, teaching and the generation of material culture traditions. *World Archaeology*, 40, 316–331.

Terkel, J. (1996). Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In C. M. Heyes & B. G. Galef Jr. (eds.), *Social Learning in Animals: The Roots of Culture* (pp. 17–48). San Diego, CA: Academic Press.

Thorndike, E. L. (1898). Animal intelligence: an experimental study of the associative process in animals. *Psychological Review Monographs, 2, No. 8.*

Thorndike, E. L. (1911). *Animal Intelligence.* New York: Macmillan.

Thornton, A. & K. McAuliffe. (2006). Teaching in wild meerkats. *Science, 313,* 2227–2229.

Thornton, A. & N. Raihani. (2008). The evolution of teaching. *Animal Behaviour,* 75, 1823–1826.

Thorpe, W. H. (1963). *Learning and Instinct in Animals.* London: Methuen.

Tomasello, M. (1990). Cultural transmission in tool use and communicatory signaling of chimpanzees? In S. Parker & K. Gibson (eds.), *Comparative Developmental Psychology of Language and Intelligence in Primates* (pp. 274–311). Cambridge, UK: Cambridge University Press.

Tomasello, M. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (eds.), *Chimpanzee Cultures* (pp. 301–317). Cambridge, MA: Harvard University Press.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef Jr. (eds.), *Social Learning in Animals: The Roots of Culture* (pp. 320–346). San Diego, CA: Academic Press.

Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology,* 28, 509–529.

Tomasello, M. (2009). The question of chimpanzee culture, plus postscript (chimpanzee culture, 2009). In K. N. Laland & B. G. Galef (eds.), *The Question of Animal Culture* (pp. 198–221). Cambridge, MA: Harvard University Press.

Tomasello, M., S. Savage-Rumbaugh, & A. C. Kruger. (1993). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development,* 64, 1688–1705.

Tuttle, M. D. & M. J. Ryan. (1981). Bat predation and the evolution of frog vocalizations in the neotropics. *Science,* 214, 677–678.

Vaesen, K. (2011). The cognitive basis of human tool use. *Behavioral and Brain Sciences,* 35, 203–218.

van Schaik, C. P., M. Ancarenaz, G. Borgen, B. Galdikas, C. D. Knott, I. Singleton, A. Suzuki, S. S. Utami, & M. Merrill et al. (2003). Orangutan cultures and the evolution of material culture. *Science,* 299, 102–105.

Visalberghi, E., & D. Fragaszy. (1990). Do monkeys ape? In S. T. Parker & K. T. Gibson (eds.), *Language and Intelligence in Monkeys and Apes* (pp. 247–273). New York: Cambridge University Press.

von Frisch, K. (1967). *The Dance Language and Orientation of Bees.* Cambridge, MA: Belknap Press.

West, M. J. & A. P. King. (1996). Social learning: Synergy and song birds. In C. M. Heyes & B. G. Galef Jr. (Eds.) *Social Learning in Animals: The Roots of Culture* (pp. 155–178). San Diego, CA: Academic Press.

behavior in the black rat (*Rattus*
:ds.), *Social Learning in Animals:*
, CA: Academic Press.
)erimental study of the associative
ographs, 2, No. 8.
York: Macmillan.
in wild meerkats. *Science, 313,*

n of teaching. *Animal Behaviour,*

imals. London: Methuen.
il use and communicatory signal-
son (eds.), *Comparative Develop-*
nce in Primates (pp. 274–311).
s.
:e culture. In R. W. Wrangham,
. Heltne (eds.), *Chimpanzee Cul-*
ird University Press.
: B. G. Galef Jr. (eds.), *Social Learn-*
6). San Diego, CA: Academic Press.
for culture. *Annual Review of*

:e culture, plus postscript (chim-
. G. Galef (eds.), *The Question of*
MA: Harvard University Press.
ger. (1993). Imitative learning of
, and enculturated chimpanzees.

i and the evolution of frog vocal-
-678.
i tool use. *Behavioral and Brain*

ldikas, C. D. Knott, I. Singleton,
003). Orangutan cultures and the
02–105.
:ys ape? In S. T. Parker & K. T.
Monkeys and Apes (pp. 247–273).

entation of Bees. Cambridge, MA:

5ynergy and song birds. In C. M.
:g *in Animals: The Roots of Culture*
ress.

White, D. (2004). Influences of social learning on mate-choice decisions. *Learning and Behavior, 32,* 105–113.

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature, 437,* 52–55.

Whiten, A. (2009). The identification and differentiation of culture in chimpanzees and other animals: from natural history to diffusion experiments. In K. N. Laland & B. G. Galef Jr. (eds.), *The Question of Animal Culture* (pp. 99–124). Cambridge, MA: Harvard University Press.

Whiten, A. & D. Custance. (1996). Studies of imitation in chimpanzees and children. In C. M. Heyes & B. G. Galef Jr. (eds.), *Social Learning in Animals: The Roots of Culture* (pp. 291–318). San Diego, CA: Academic Press.

Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, et al. (1999). Cultures in chimpanzees. *Nature, 399,* 682–685.

Whiten, A. & R. Ham. (1992). On the nature and evolution of imitation in the animal kingdom. *Advances in the Study of Behavior, 21,* 239–283.

Whiten, A., R. A. Hinde, C. B. Stringer, & K. N. Laland. (2011). Culture evolves. *Philosophical Transactions of the Royal Society of London, B, 366,* 935–1187.

Whiten, A., V. Horner, C. A. Litchfield, & S. Marshall-Pescini. (2004). How do apes ape? *Learning and Behavior, 32,* 36–52.

Whiten, A., V. Horner, & S. Marshall-Pescini. (2003). Cultural panthropology. *Evolutionary Anthropology, 12,* 92–105.

Whiten, A. & A. Mesoudi. (2008). Establishing an experimental science of culture: Animal social diffusion experiments. *Proceedings of the Royal Society of London, B, 363,* 3477–3488.

Whiten, A., J. Moseley, P. Milner, & I. Agiobukemmer. (1980). Infant education in Britain and Nigeria. *Bulletin of the British Psychological Society, 33,* 99.

Yoerg, S. I. (1991). Social feeding reverses learned flavor aversions in spotted hyena (*Crocuta crocuta*). *Journal of Comparative Psychology, 105,* 185–189.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In C. M. Heyes & B. G. Galef Jr. (eds.), *Social Learning in Animals: The Roots of Culture* (pp. 221–244). San Diego, CA: Academic Press.

Zentall, T. R. (2004). Action imitation in birds. *Learning & Behavior, 32,* 15–23.

Zentall, T. R. & B. G. Galef, Jr. (Eds.). (1988). *Social Learning: Biological and Psychological Perspectives.* Hillsdale, NJ: Lawrence Erlbaum Associates.