Social Learning in Animals: Empirical Studies and Theoretical Models

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The last two decades have seen a virtual explosion in empirical research on the role of social interactions in the development of animals' behavioral repertoires, and a similar increase in attention to formal models of social learning. Here we first review recent empirical evidence of social influences on food choice, tool use, patterns of movement, predator avoidance, mate choice, and courtship, and then consider formal models of when animals choose to copy behavior, and which other animals' behavior they copy, together with empirical tests of predictions from those models.

Keywords: social learning, tradition, public information

Many of the biologically important decisions that an animal must make can be affected by its observation of the behavior of others. The foods an individual chooses to eat, the motor patterns it uses to gain access to food, the time it spends foraging in a patch, the predators it avoids, the individuals it selects as sex partners—all can be affected by observation of others of its species. Although theory suggests that adopting the behavior of others may not always be in the best interests of an animal observing the actions of conspecifics (see below), the benefits of social learning, particularly to naive young animals, should most often outweigh any potential costs.

Many of the things that young animals have to learn must be learned rapidly. A fledging bird or weaning mammal, venturing from the site where it has been protected and sustained by adults of its species, has to learn to avoid predators before it is eaten by one. It has to learn to select a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrient, and without ingesting harmful quantities of toxins. A naive young animal, newly recruited to a population and faced with such challenges, would be well advised to take advantage of opportunities provided by interaction with adults of its species.

Almost by definition, adults are individuals that have acquired patterns of behavior allowing them to avoid predators and the ingestion of toxins, to select an adequate diet, and to find water and safe refuges. Most important, adults are doing all of these things in the environment where the juveniles with which they interact are struggling to achieve independence. Consequently, to the extent that ignorant

juveniles can use the behavior of adults to guide development of their own behavioral repertoires, juveniles should often be able to acquire necessary responses to the demands of the particular locales in which they are living without incurring many of the costs associated with individual trial-and-error learning.

Intuitively, it seems reasonable to hypothesize that members of colonial species, such as Norway rats (*Rattus norvegicus*) or Mongolian gerbils (*Meriones unguiculatus*), should be more likely to engage in social learning than members of relatively solitary species, such as golden hamsters (*Mesocricetus auratus*). Lupfer and colleagues' (2003) recent comparative study of social learning of food preferences by golden and dwarf hamsters (*M. auratus* and *Phodopus campbelli*) was based on the assumption that relatively social and asocial species of hamster would differ in their reliance on social learning in developing food preferences. However, such a prediction ignores the fact that, at least in the mammals and birds (which are the primary focus of this overview), adult members of almost all species, whether social or solitary, interact with their offspring during the period in their lives when

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social learning might be predicted to be of greatest importance. Consequently, a dependence on socially acquired information in selecting foods might have been expected, at least as an ontogenetic adaptation, in solitary as well as in social species of hamster. In fact, Lupfer and colleagues (2003) found that, although adult golden hamsters did not influence one another's food preferences, 4-week-old golden hamster pups showed a significantly enhanced preference for foods that their mother was eating. Such data suggest that ontogeny, as well as phylogeny, may be of importance in determining the distribution of social learning across species, and that dependence on social learning may vary in predictable ways throughout the lives of animals.

As Coussi-Korbel and Fragaszy (1995) have proposed, social learning depends on social dynamics that govern the relationships among individuals. To the extent that acquisition of information about the activity of another is affected by proximity to that other, all else being equal, both tolerance of knowledgeable individuals for the presence of others and proximity seeking by the naive should affect the probability that the naive will acquire the behavior of the knowledgeable. We thus agree with Lefebvre and Palameta (1988) and Coussi-Korbel and Fragaszy (1995), both that occurrence of social learning is more likely to reflect a species' ecology and social organization than its phylogeny, and that effects of social dynamics in modulating and directing social learning are, though little studied, of fundamental importance in understanding when and how social learning will occur.

The relatively recent realization of the potential importance of social learning in the lives of animals has led to a near-exponential increase in the number of empirical investigations concerned with the effects of social interactions on the acquisition and performance of behavior. Expansion in the empirical data has been accompanied by substantial progress in development of formal models predicting when and from which individuals information should be acquired socially. Here, we first review critically a few of the many instances that, it has been suggested, demonstrate the influence of social learning on the development of biologically important behaviors of free-living animals. We then discuss briefly recent theoretical developments and a sample of experiments that test predictions from formal models.

Learning what to eat: Poison avoidance and food choices of Norway rats

Fritz Steiniger (1950), an applied ecologist who attempted to enhance the efficiency of procedures used to control rodent pests, discovered many decades ago that when he repeatedly introduced the same poison bait into the territory of a colony of wild Norway rats, his efforts at rodent control failed dismally. Although there was a decline in the size of a pest population when a poison bait was first introduced, colonies repeatedly given the same bait soon returned to their initial size. Most colony members would eat a lethal dose of toxin when it was first introduced. However, a few individuals ate only a small amount of bait on their first encounter, became

ill, but did not perish. These surviving rats learned from that single experience of illness to associate the poison bait with its deleterious effects, and they would eat no more of it.

Even more discouraging for Steiniger's attempt at rodent control, young rats born to survivors totally rejected the poison bait that their elders had learned to avoid, and would not even taste it for themselves. Steiniger (1950) hypothesized that the aversion learned by adult survivors was transmitted to their young through warning pheromones that the adults placed on the poison bait. However, we now know that, to the contrary, young Norway rats learn from their elders not which potential foods to avoid eating but which foods to eat, and are very reluctant to ingest foods to which older members of their colony have not introduced them (Galef and Clark 1971). The result is the same as if adults directly dissuaded their young from eating a known poison: the avoidance, by new recruits to a population, of any food that its established members are not eating. However, the behavioral mechanism is quite different from that which Steiniger hypothesized.

Possible prenatal influences on food choice. Even before young rats are born, they can acquire information from their female parent about at least some of the foods that she is eating. For example, Hepper (1988) fed garlic to pregnant rats late in gestation and, shortly after their litters were delivered, gave the young for rearing to foster dams that had never eaten garlic. When the pups were tested 12 days later, they preferred the odor of garlic to that of onion, whereas rats gestated by mothers eating a garlic-free diet were indifferent when offered the same choice. Smotherman (1982) found that adult rats that had been exposed while in their dam's uterus to apple juice injected into her amniotic fluid and offered a choice between apple juice and water showed a greater preference for apple juice than pups whose dams had received injections with water while pregnant. It has yet to be shown that either weanlings or adults naturally exposed to food-related cues before birth show an enhanced preference for food with a flavor that was experienced in utero.

Flavor cues in mother's milk. It has, however, been clearly established, first, that flavors of foods that a female rat (or human) eats while lactating can affect the flavor of her milk, and second, that exposure to food flavors in mother's milk affects the food preferences of young at weaning. Galef and Sherry (1973) took rat pups suckled by a dam maintained on an unflavored diet, fed them milk expressed by hand from a lactating rat maintained on a distinctively flavored diet, and then made the pups ill by injection with a mild toxin. At weaning, these pups showed an aversion to the distinctively flavored diet. Weaning rat pups also showed an enhanced preference for a distinctively flavored food eaten by a lactating female from which they had nursed for several hours, but did not show a similar enhanced preference after attempting to nurse from a female that had eaten the same flavored food and had been induced to act maternally, but did not give milk.

Effects while weaning. Wild rat pups and their dams living in a room-sized enclosure, and observed while each took its first meal of solid food outside the nest, ate at the same time and place at which an adult was eating (Galef and Clark 1971), though the temporal and spatial distribution of adult feeding made such coincidence extremely unlikely. When adults are at a distance from the nest, visual cues are important in guiding young to them (Galef and Clark 1971). However, as adult rats feed, they also deposit olfactory cues in and around foods, and such residual markers are highly attractive to pups (Galef and Heiber 1976, Laland and Plotkin 1991).

Effects after weaning. Perhaps most interesting, after a naive rat (an observer) interacts for a few minutes with a conspecific that has recently eaten some food (a demonstrator), the observer shows an enhanced preference for whatever food its demonstrator ate (Galef and Wigmore 1983). Such social influence on observers' food preferences is considerably stronger and longer lasting than might be expected. These interactions can affect food choices for a month or more, and overcome both poison-induced learned aversions and a species-typical aversion to peppery food (Galef 1989, Galef and Whiskin 2003).

Simultaneous exposure of an observer rat to the odor of a food on a demonstrator rat's breath and to carbon disulfide, a normal constituent of rat breath, causes observers to acquire an enhanced preference for demonstrators' diets (figure 1). The effect of a demonstrator rat on an observer's food preferences can be mimicked by exposing a rat to a piece of cotton batting powdered with a flavored diet and moistened with carbon disulfide solution; this effect is not achieved if the food-scented cotton batting is moistened only with water instead of carbon disulfide (Galef et al. 1988). Humans, who, like rats, have trace amounts of carbon disulfide on their breaths, can also serve as effective "demonstrators" for observer rats.

Learning how to eat: Roof rats, Caledonian crows, chimpanzees, and Galápagos finches

Simple observation of the behavior of a range of animals in their natural environments suggests that social learning is important in development of the motor patterns that they use to acquire food. The results of further studies are sometimes consistent and sometimes inconsistent with that hypothesis.

Roof rats opening pinecones. The pine forests of Israel are inhabited by colonies of roof rats (*Rattus rattus*) that subsist on a diet consisting almost entirely of pine seeds and water (Terkel 1996). Laboratory studies of rats taken from such colonies have shown that the rats' feeding method, which allows them to recover more energy from pine seeds than is required to gain access to them by removing the tough scales that protect the seeds, depends critically on appropriate exploitation of the physical structure of pinecones. Scales from the bottom of a cone must be removed first. Then the scales

*Figure 1. Norway rats (*Rattus norvegicus*) sniffing one another's breath to determine what food a conspecific has recently eaten. The rats subsequently show an enhanced preference for that food that lasts for weeks. Photograph: Bennett G. Galef Jr.*

spiraling around the cone's shaft from base to apex must be removed in succession (figure 2; Terkel 1996).

Only 6 of 222 hungry adult rats, captured outside pine forests and offered pinecones to eat while in captivity, learned the efficient, spiral pattern of scale removal, whereas essentially all rats acquired the technique if they were reared by dams captured in pine forests that demonstrated the efficient method of pinecone opening for young they reared. Further experiments demonstrated that when young rats finished stripping the scales from cones that adult rats (or humans using pliers to mimic the pattern of scale removal by efficient rats) had started to strip, their experience resulted in more than 70% of them acquiring the efficient method (Terkel 1996).

The tradition of pinecone opening seen in the Israeli rats is particularly interesting because it has allowed roof rats to thrive in an environment that would otherwise be closed to them. Social learning of food preferences may similarly allow Norway rats to invade areas where necessary nutrients are difficult for an individual to locate, because once one rat has identified a valuable food, it is much easier for others to find that food.

*Figure 2. Roof rat (*Rattus rattus*) efficiently stripping scales from a pinecone to reveal the pine seeds that the scales protect. This socially transmitted behavior has become a behavioral tradition among the roof rats that live in pine forests in Israel, where it enables the rats to survive in a portion of the environment that would otherwise be closed to them. Photograph: Terkel (1996), reprinted by permission of Academic Press.*

Manufacture and use of probing tools by Caledonian crows.

The manufacture and use of probing tools by birds and primates illustrates some of the complexities associated with identifying social learning processes in natural populations of animals, and reveals some of the difficulties in demonstrating conclusively that behavior that appears to be social transmitted may not be. Caledonian crows (*Corvus moneduloides*) on Grande-Terre Island, New Caledonia, manufacture three types of tools from the leaves of the pandanus tree (wide tools, narrow tools, and stepped tools) and use them to probe for insects (Hunt 2000, Hunt and Gray 2002). Relatively sophisticated stepped tools are stiff at the base and pointed at the end that is used to probe for insects, and appear better suited for that use than the simpler wide or narrow tools.

The distribution of tool types across Grande-Terre can be determined because each tool is cut from a living leaf, leaving behind an outline of the removed tool. In study sites in the north of Grande-Terre, 98% of tools were stepped, whereas in the south of the island roughly equal numbers of the three tool types were found. Just to the north of the southernmost study sites, narrow and stepped tools were found in equal numbers, and wide tools were rare.

Circumstantial evidence is consistent with Hunt and Gray's (2002) conclusion that although "we do not have direct evidence for social transmission of tool design among crows, this seems probable" (p. 873). Distribution of tool types is not correlated with any ecological factor that Hunt and Gray have measured, and the absence of simpler wide or narrow tools in the north suggests that individual crows do not learn to make more sophisticated tools by gradual trial-and-error learning (Hunt and Gray 2002). However, there are possible problems. For example, if the geographic pattern of tool manufacture is a consequence of social learning, why is only a single tool type used in the north, whereas several types are produced in the south? Possibly, different tools are used to hunt different prey, and prey distribution is responsible for the observed pattern of tool production. Furthermore, a recent study reveals that when Caledonian crows were hand-reared under conditions that provided no opportunity to observe an adult conspecific manufacture or use tools, they spontaneously developed tool-manufacturing and tool-using behaviors, though none of the captive crows' initial productions resembled the complex tools manufactured by conspecifics in the wild (Kenward et al. 2005). Further, the possibility of genetic differences between populations of crows in the north and south of Grande-Terre, which might affect tool manufacture, has yet to be explored.

Tool use by chimpanzees.

Recent studies of geographic variation in chimpanzees' construction and use of tools to dip for driver ants, long believed to be a result of social traditions in chimpanzee (*Pan troglodytes*) populations (Whiten et al. 2001), also suggest a more mundane explanation. Chimpanzees at Gombe, in East Africa, forage for driver ants using a long wand, held in one hand, that they dip into a group of ants and then withdraw as ants stream up the wand to attack. A feeding chimp then sweeps the wand with its free hand, collecting a loose ball of ants that it pops into its mouth. At Tai, in West Africa, chimpanzees use a short stick to collect driver ants and then pull the stick through their mouths to ingest the ants. At Bossou, in West Africa, chimps use both short-stick and wand techniques, and use the former method more frequently than the latter, although the short-stick method results in the capture of far fewer ants per minute. Like Boesch and Boesch (1990) and McGrew (1992) before them, Whiten and colleagues (2001) were satisfied that ecological differences between the Gombe and Tai sites could not explain this variation in behavior. Furthermore, Whiten and colleagues concluded that "it is difficult to see how such behaviour patterns could be perpetuated by social learning processes simpler than imitation" (p. 685).

Recently, Humle and Matsuzawa (2002) discovered that both the length of tool used by chimps at Bossou and the technique chimps use to strip ants from tools are fully predicted by the behavior of the ants. Wands, and the pull-through-the-hand method of feeding, are used when ants are aggressive or dense, and short sticks and the pull-through-the-mouth method of feeding are employed when ants are less aggressive or are away from their bivouacs. Equally telling, the frequency with which individuals use each of the two methods is related to their ages, and mothers and their offspring do not tend to use the same method.

What appeared to be a clear case of social learning may have other explanations. Possibly the different ant-dipping techniques used by chimpanzees at Gombe and Tai reflect differences in the behavior of the driver ants that chimpanzees feed upon on opposite sides of the African continent, and are learned individually by trial and error. Humle and Matsuzawa's (2002) data suggesting that the best-documented case of tradition in chimpanzees may be a consequence of differences in local ecology rather than a product of social learning suggests that further scrutiny of other putative chimpanzee traditions is needed.

Obviously, we have some way to go before we understand the development of differences in behavioral repertoires of free-living populations and the role, if any, of social learning in producing such differences. The use of tools by woodpecker finches (*Cactospiza pallida*) in the Galápagos Islands provides a relevant example.

Development of tool use in Galápagos woodpecker finches.

Galápagos woodpecker finches are famous for their use of twigs and cactus spines as tools to push or lever arthropods out of crevices in bark. If such a complex pattern of behavior were observed in a cetacean or primate, it would surely be viewed as a possible tradition resting on social learning. However, when Tebbich and colleagues (2001) examined the development of tool use by woodpecker finches, they found no evidence that social learning played a role. Juveniles used tools to look for prey even if they had never seen tool use demonstrated, 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 by observation of conspecifics demonstrating the technique. The investigators interpreted their findings as indicating that Galápagos woodpecker finches are predisposed to learn to use tools by trial and error, but only during a sensitive period early in development.

One message from such investigations of tool use is that, although it is tempting to attribute complex behaviors observed in free-living animals (especially complex behaviors found in only some populations of our closest relatives) to social learning and tradition, these attributions must be considered provisional until the development of such behaviors is better understood (Galef 1992). A sobering and relevant observation is that several species of ants use, and even manufacture, foraging tools (Hansell 1984, Holldobler and Wilson 1994).

Learning how to get to a resource: Coral reef fishes and guppies

Successive generations of the blue-headed wrasse (*Thalassoma bifasciatum*) use the same site for mating, although the chosen location is not in any observable way superior to other sites that wrasses do not use for spawning. Warner (1988) trapped all members of a population of wrasses, removed them, and replaced them with individuals trapped in a different location. The newcomers selected a different mating site from that used by the original population, and the new site was used by several generations in succession.

Large juvenile French grunts (*Haemulon flavolineatum*) in the Virgin Islands form daytime resting schools at specific coral heads, and at dusk and dawn all migrate along the same apparently featureless routes from schooling to foraging sites and back. Both schooling sites and migration paths may persist for as long as 3 years, although no individual remains a member of a school for more than 2 years. Helfman and Schultz (1984) transplanted grunts into schools and allowed the transplants to follow their foster school along their daily migration routes to and from schooling and foraging sites. When all the original members of the foster school were subsequently removed, the transplants continued to use the migration routes of their foster school and returned to the schooling site their foster school had used. Control fish that had not been given the opportunity to learn from the foster school did not share either its migration routes or its schooling sites. By virtue of their experimental manipulations, these studies of reef fishes provide compelling evidence for social learning processes underlying selection of mating sites and use of schooling and foraging sites and paths between them.

Social determination of paths to foraging sites has been explored in the laboratory by Laland and his students, who have examined closely effects of social influence on guppies' (*Poecilia reticulata*) choices of paths to food. When tested alone, adult female guppies that had shoaled with trained conspecifics as they swam to food used the same route that their trained fellows had used, even if the route taken by the trained shoal was longer and more energetically costly than alternative routes (Laland and Williams 1997, 1998).

Learning what to fear: Rhesus monkeys, European blackbirds, and fishes

Because predator avoidance requires individuals to avoid a variety of different stimuli the first time that they are encountered, understanding how animals learn to avoid predators has provided a challenge both to ethologists studying "instinctive" responses to stimuli and to psychologists interested in individual learning. Social learning may provide at least part of the answer.

Laboratory-born and reared rhesus monkeys (*Macaca mulatta*) show no fear of snakes or of snakelike objects, whereas their wild fellows react vigorously when exposed to the same stimuli that elicit avoidance and fear in their wild-born fellows. Cook and Mineka (1989) found that laboratory-born monkeys avoided snakes for months after watching, either directly or on television, while a wild-reared monkey responded to a snake. Having established that the monkeys were responsive to television images, the researchers edited videotapes so that it appeared to naive, laboratory-born monkeys that wild-born individuals were responding fearfully not to a snake, but to a flower. The laboratory-born monkeys never learned to fear flowers, though they would learn to avoid snakes by watching televised images of conspecifics' responses to snakes. Apparently, the monkeys are predisposed to learn socially to fear some stimuli, but not others. Similarly, although European blackbirds (*Turdus merula*) will respond to either a stuffed bird or a plastic bottle as though it were a predator after hearing a conspecific produce mobbing vocalizations in response to either, the socially learned response to a stuffed bird is considerably stronger than that to a bottle (Curio 1988).

Various species of fish can learn to avoid a previously neutral stimulus after experiencing that stimulus together with an alarm substance released when the skin of a conspecific is injured (Brown 2003). As in macaques and blackbirds, conditioning is stronger when the alarm substance is associated with a potential predator than with a harmless object (Chivers and Smith 1994).

In macaques, blackbirds, and fishes, an individual that has learned socially to respond to a previously neutral stimulus as if it were a predator can serve as a model for other naive individuals. By iterating this procedure, a tradition of response can be created in a population.

Mate-choice copying in guppies and quail

Lee Alan Dugatkin and his collaborators (Dugatkin 1992, Dugatkin and Godin 1993, Kirkpatrick and Dugatkin 1994) conducted a series of studies of mate-choice copying in first-generation wild-caught Trinidadian guppies, a species that, in the wild, gathers in mixed-sex shoals in clear water, thus allowing for possible observation by the guppies of the mating behavior of others. Dugatkin (1992) provided focal female guppies with the opportunity to view two target males confined with transparent partitions at opposite ends of a small aquarium. A second female was then placed with one male, and the focal female was allowed to watch the pair

court and mate, while the male confined at the opposite end of the aquarium remained alone. In a subsequent test of the focal female's preference, females tended to remain closer to whichever male they had seen mating, and control groups showed that this bias could not be explained by a tendency of females to join a group or to choose a male that they had seen engage in courtship. However, the tendency of females to copy the mate choices of others may be specific to the population that Dugatkin studied. Others using domestic guppies or guppies from Australia have not found a preference of focal females for males seen mating, though female fishes of species other than guppies have been found to copy the mate choices of conspecifics (Brown and Laland 2003).

Studies conceptually similar to those of Dugatkin with guppies have been undertaken using Japanese quail (*Coturnix japonica*) as subjects (Galef and White 1998, White and Galef 2000a). The results of these experiments are similar to those that Dugatkin reported in guppies, with focal females showing an enhanced tendency to affiliate with a male seen courting and mating with a model female. Focal female quail are also more likely to lay fertilized eggs after mating with a male they have seen court and mate with another female (figure 3) (Persaud and Galef 2005). Further, a female observing a courting male with a distinguishing characteristic subsequently shows an enhanced preference not only for him but also for other males that have the same distinguishing feature (White and Galef 2000a). Consequently, social influences in quail have the potential to affect the evolution of sexually selected traits in conspecific males (Brooks 1998), as anticipated by theoretical models (Kirkpatrick and Dugatkin 1994, Laland 1994).

Figure 3. Japanese quail (Coturnix japonica). A female Japanese quail watches a male mating with another female. She will subsequently show an enhanced preference for him, and will allow him to fertilize more of her eggs than if she had not watched him mate. Photograph: Bennett G. Galef Jr.

While focal female quail show a relatively long-lasting increase in their tendency to affiliate with males they have seen mating, focal male quail show a transient avoidance of a female after watching her mate with another male. Male avoidance of a female seen mating lasts approximately as long as an inseminated female's eggs are not available for fertilization after her first mating. The difference in direction and duration of the response of male and female quail to watching a potential partner mate with a member of the opposite sex is consistent with the notion that adaptively specialized behavioral processes mediate social effects on mate choice in the species (White and Galef 2000b).

Learning how to court: Song and courtship in brown-headed cowbirds

Brown-headed cowbirds (*Molothrus ater*) are obligate brood parasites whose young are always reared by members of other species. Late in the summer, when juvenile cowbirds become independent of their foster parents, they join flocks consisting primarily of other juvenile cowbirds, and then spend the winter as members of very large mixed-species flocks.

In captivity, birds captured in different parts of the United States prefer as mates members of the opposite sex that were captured in the same place that they were. The development of differences in courtship behavior that are responsible for this assortative mating has been thoroughly investigated (Freeberg 2004). Songs of males from different geographical areas are structurally distinct, and females are more responsive to songs of males from their own population than to songs of males from other populations.

In a conceptually straightforward but procedurally complex set of experiments, Freeberg (1996) showed that young males captured in one location and then maintained in an aviary with adults from a different location developed songs typical of their cage mates rather than of their natal populations. Similarly, females maintained in an aviary with adults from a location different from the one where they were captured developed a preference for songs typical of their cage mates, and subsequently paired preferentially with males singing similar songs. Male song patterns, female preference for songs, and a tendency to mate with those engaging in socially determined courtship behavior could be transmitted across generations. For example, young males captured from one area and reared with adult males from a second could serve as models for their own young, inducing those young to behave as did the males that reared their parents.

Analyses of the behavioral processes supporting such effects have revealed a complex of social effects of adults on one another's behavior as well as on the behavior of juveniles. For example, the same songs that females find attractive during the breeding season are responded to at other times of year with a "wing-stroke" display. After a female gives a wing stroke in response to one of the songs in a male's repertoire, he repeats it three or four times in succession, thus violating a basic rule of male cowbird song production. Normally, a male sings all of the songs in his repertoire one after the other

without repetition. Seeing a female give a wing stroke in response to a particular song increases the frequency with which the male sings that song both outside and during the breeding season, thus increasing his breeding success (West and King 1988).

Male cowbird song production is also affected by interaction with other male cowbirds. Those songs that are most effective in eliciting copulations from female cowbirds are also most effective in eliciting attacks by male cowbirds. Consequently, only dominant males in a group can afford to sing the song variants that are most effective in eliciting copulations from females (West and King 1980).

The adaptive significance of social learning

Learning is a set of complex ontogenetic processes that allows animals to acquire, store, and subsequently use information about the environment. This information complements genetic information, allowing animals to fine-tune their behavior to the idiosyncratic properties of their local circumstances to a degree that would be impossible on the basis of genetically coded information. For instance, some factors in the environment change many times within the life span of an individual, and natural selection acting on genetic variation in a population cannot furnish individual organisms with specific adaptations for each environmental circumstance. What natural selection can do is select for information-acquiring systems that permit an individual to adjust its behavior in a broadly adaptive manner to changes in its environment that occur during its life span.

Many species have evolved a capacity to use information provided by others to guide their learning. Experienced others, such as parents, provide a reservoir of potentially useful behaviors. Adopting behaviors directly from this reservoir allows naive individuals to shortcut the many iterations of trial and error necessary for most individual learning, and to move directly to solutions previously tested by others.

The general capability for social learning is not only an adaptation, but one of indubitable significance in the evolution of complex behavior in vertebrates. However, it is important to distinguish between the general capability for social learning and any specific instance of use of social cues to guide behavioral development. In the latter case, whether the use of available social information will prove adaptive depends on the relative costs and benefits of social and asocial learning. In fact, evidence is accumulating, from studies of fish, birds, and mammals, that animals will ignore social information under specific circumstances (Kendal et al. forthcoming). For instance, nine-spined sticklebacks (*Pungitius pungitius*) will ignore public information about the profitability of food patches if they have reliable, up-to-date personal information from their own foraging, but will switch to exploiting public information if their personal information is unreliable or outdated (Van Bergen et al. 2004). It seems that animals will switch conditionally between reliance on social and asocial information, according to their respective reliability and cost.

Although it might seem intuitively that learning from others rather than incurring whatever costs are associated with the trial and error of individual learning would be adaptive under almost all circumstances, indiscriminately copying the behavior of others is unlikely to be an adaptive strategy, as several theoreticians have pointed out (Boyd and Richerson 1985, Laland 2004). Models based on evolutionary game theory, which treat individual learners as information producers and social learners as information scroungers, reveal that social learners reap greater rewards than producers only when scroungers are relatively uncommon in a population (Giraldeau and Caraco 2000). Assuming some degree of change in the environment, if everyone were scrounging information and no one was producing it, nobody would learn anything useful by copying. At equilibrium, the mix of producers and scroungers in a population should be such that the payoffs for producing and scrounging information are equal.

Models based on the evolution of social learning reveal similarly that copying results in higher fitness than individual learning only when copying is relatively unusual and most potential demonstrators are tracking the environment (Boyd and Richerson 1985). All models agree that animals should be selective about what other animals they copy and when (Laland 2004).

When to copy. Because there is a trade-off between acquiring accurate but costly information (such as learning to avoid a predator by personal experience) and possibly less accurate, but cheaper, socially acquired information, theoretical models reveal that individuals should adopt the strategy of copying when individual learning is costly (Boyd and Richerson 1985, 1988). This theoretical finding is supported by some empirical evidence. For example, Templeton and Giraldeau (1996) found that European starlings (*Sturnus vulgaris*) used observation of the foraging success of others to determine whether to remain in or to leave a foraging patch only when information about patch quality was difficult to acquire by personal sampling.

Further support for use of a "copy when asocial learning is costly" strategy comes from a comparative study of public information use in two species of stickleback. Van Bergen and colleagues (2004) found that nine-spined sticklebacks, for which personal sampling of food-patch quality is potentially costly because their weak structural defenses leave them vulnerable to predation, could gauge the foraging success of other fish feeding at patches and use this information to guide their subsequent patch choices. In the same situation, the closely related three-spined sticklebacks (*Gasterosteus aculeatus*), which have large spines and robust pelvic plating that make them less vulnerable to predation than nine-spined sticklebacks and render the direct sampling of food sites relatively cheap, did not use public information.

An alternative approach to modeling the factors that should determine whether an individual should learn socially or depend upon its personal experience focuses on possible differences in the environment to which a potential model has

learned to respond and the environment facing a potential social learner. Boyd and Richerson (1988) showed that animals should be more likely to rely on social learning as the probability increased that they and potential demonstrators shared an environment. In rapidly changing environments, dependence on social learning would prevent effective tracking of environmental affordances. Consequently, copying should be favored more frequently in moderately stable than in rapidly changing environments (Laland et al. 1993). Galef and Whiskin (2004) maintained rats either under standard laboratory conditions or in a rapidly changing environment where subjects were moved daily to new cages, and each day were offered an unfamiliar food for varying durations at different times of day. Subjects in both groups were then given the opportunity to learn a food preference socially. Consistent with the above prediction, although subjects maintained in both stable and variable environments acquired an enhanced preference for the food that their respective demonstrators ate, the food choices of subjects maintained in the variable environment were less affected by interaction with demonstrators than were the food choices of subjects maintained in the stable environment.

When to keep engaging in copied behavior. Most models are concerned with the conditions under which social learning should occur, and assume a correspondence between the acquisition of information and its expression in behavior. However, when this distinction between acquired knowledge and expressed behavior has been subject to theoretical investigation, models reveal that their frequencies can be discordant (Kendal 2002). It is often difficult to determine whether the failure of an individual to behave similarly to a potential model results from failure to learn socially or from failure to perform a behavior after it has been learned by observing a model. One set of experiments based on formal modeling, by Luc-Alain Giraldeau and his colleagues, has been particularly successful in drawing that distinction.

Theoretical models typically assume that any member of a group of social foragers should scrounge food produced by others when possible, unless scrounging entails significant costs (Giraldeau and Caraco 2000). The observation that dominant members of a group of pigeons (*Columba livia*) are more likely to scrounge than are their subordinates (Giraldeau and Caraco 2000) is consistent with the hypothesis that, at least for dominants, scrounging produces greater net rewards than does producing.

Giraldeau and Lefebvre (1987) found that pigeons that had learned socially to produce seed by removing the stopper from a test tube would switch from producing to scrounging and back again as a function of whether there were producers active in the population. Scroungers and producers maintained a frequency-dependent balance, with the proportion of scroungers decreasing as the producers' share of production increased (Giraldeau and Beauchamp 1999). Clearly, the frequency of performance of socially learned and alternative behaviors was determined by the relative payoffs of each type of behavior.

Perhaps more interesting, Giraldeau and Lefebvre (1987) found that pigeons that scrounged food from conspecific demonstrators removing stoppers (a behavior that was unlikely to be learned individually) were less likely to open containers when their demonstrators were absent than were pigeons that had watched demonstrators open food containers but could not scrounge the food that their demonstrators produced. Pigeons appeared unable simultaneously to scrounge and to learn by observation. However, other evidence suggests that, consistent with information-sharing models, individuals can simultaneously scrounge and learn socially. Giraldeau and Lefebvre (1987) found that when no demonstrator was present, more pigeons opened containers after simultaneously observing a model produce food and scrounging some of the food produced than did pigeons that had never seen a demonstration of container opening.

Which others to copy. Mathematical analyses exploring the evolution of social learning have concluded that both humans and animals should be selective not only about when they copy behavior but also about which other people or animals they copy (Laland 2004). Considerable modeling effort has gone into exploring the relative effectiveness of various strategies for choosing individuals as models.

Copying the majority. Theoretical analyses suggest that, most often, when evolution favors reliance on social learning, an individual should copy the behavior exhibited by the majority of potential models (Boyd and Richerson 1985). Indeed, studies in a range of species, from guppies (Laland and Williams 1997) to Norway rats (Chou and Richerson 1992), have shown the probability that an observer will adopt a behavior increases monotonically with the proportion of potential models exhibiting that behavior, although, strictly speaking, "copying the majority" requires disproportionate copying of the behavior of members of the majority. Nonetheless, there is evidence that social learning processes in animals may be influenced by conformity. For example, Day and colleagues (2003) presented hidden food to shoals of guppies in an aquarium. On average, individuals in large shoals located food faster than individuals in small ones, and large numbers of fish at a food site attracted conspecifics faster than small aggregations. However, when a visual barrier required individuals to break visual contact with a shoal to locate the food source, the reverse pattern was found, with small shoals finding food more quickly. The discrepancy is explained by conformity, which facilitates social transmission in the former case, but hinders it in the latter.

Numerous strategies other than copying the majority have been explored by theoreticians: copying the successful (Boyd and Richerson 1985), copying those doing better than oneself (Schlag 1998), copying if dissatisfied with one's own performance (Schlag 1998), copying older individuals (Kirkpatrick and Dugatkin 1994), and so on. The details of

these and other models are discussed in Laland (2004). Here we are concerned only with the few that have been tested empirically.

Copying the successful. Boyd and Richerson (1985) first proposed that copying the behavior of successful individuals should be favored by natural selection, even though such a strategy may sometimes allow maladaptive traits to be copied as well as those leading to success. Ward and Zahavi (1973) proposed that birds' roosts serve as information centers where unsuccessful foragers identify successful individuals that they then follow to food. Thirty years of observation and experiment have produced few data consistent with the "information center hypothesis" in birds (Mock et al. 1988), though there are scattered data suggesting that, in some non-avian species that forage socially, unsuccessful foragers may identify successful individuals and follow them to food. For example, Wilkinson (1992), in a study of information transfer in nursing colonies of evening bats (*Nycticeius humeralis*), found, first, that adult females that had been unsuccessful in foraging tended to follow successful individuals, and second, that females that followed successful individuals from the nursing colony were subsequently more successful than females that departed alone. In studies of foraging by chimpanzees, Menzel (1974) reported that naive chimps were more likely to follow a conspecific that knew where to find food than to follow an uninformed individual, and similar findings have been described in guppies.

The term "successful" can be interpreted broadly to include relatively high social status as well as short-term success in resource acquisition. For example, Nicol and Pope (1999) report that, in domestic fowl (*Gallus gallus*), high-status individuals are more effective demonstrators than are low-status individuals, a result Nicol and Pope attributed to greater attention paid by flock members to dominant than to subordinate individuals.

Copying older individuals. Given the relative ease of designing and conducting studies of the effects of the relative age of demonstrator and observer on social learning, surprisingly few such studies have been carried out, though Kirkpatrick and Dugatkin (1994) have provided a mathematical analysis of how the evolution of male traits is affected by young females copying the mate choices of older females. Dugatkin and Godin (1993) report that smaller female guppies preferentially copy the mate choices of larger (presumably older) guppies, and Galef and colleagues (2001) found that young rats were more likely to snatch food from the mouths of their elders, and thus to acquire a preference for a food, than the reverse. However, Galef and Whiskin (2004) found that the age of demonstrators had no effect on the social transmission of food preferences at a distance from a feeding site.

Conclusions

We end this overview with a brief consideration of its limitations. Today, hundreds of researchers from around the world—with backgrounds in fields ranging from anthropology, psychology, economics, and robotics to neuroanatomy, zoology, and population and molecular biology—are actively engaged in studies, both theoretical and empirical, of the potential role of social learning in the development of the behavioral repertoires of animals. Sadly, we have been able to discuss only a small portion of that activity. Those interested in the behavior of invertebrates may have been surprised to find no mention of social foraging in eusocial insects, while students of animal communication will wonder at the very limited discussion of the development of traditions in avian or cetacean vocalization. Obviously, the vast literatures on invertebrate social learning and social influences on communication are each worthy of an overview at least as lengthy as this one.

Even our review of recent developments in the study of social learning is highly selective; it provides only a sample of the wealth of material that has been developed during the last 30 years. (For more thorough reviews, see Zentall and Galef 1988, Heyes and Galef 1996, Box and Gibson 1999, Dautenhahn and Nehaniv 2002, Fragaszy and Perry 2003, and Galef and Heyes 2004.) Although of obvious importance and considerable current interest, issues such as the relationship between social learning and innovation or between neural substrate and social learning have not been touched upon, and some contentious issues pertaining to the adaptive value of an ability to learn socially have not been addressed. Rather, we have focused on controlled studies of social-learning phenomena known to occur in natural circumstances, and on formal models of social learning and empirical tests of predictions derived from such models, because we view such work as fundamental to future development of the field. Unfortunately, to date, much of the empirical research on social learning has been conducted essentially without reference to formal theory, and theoreticians have often been little concerned with the relationship between the predictions of models and relevant empirical findings. We hope that reviews such as the present one will contribute to greater integration of theoretical and empirical approaches.
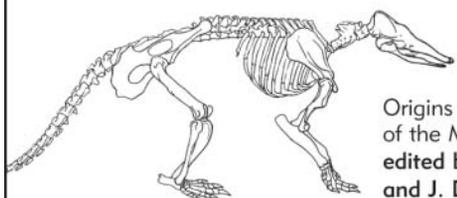
References cited

Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. Folia Primatologica 54: 86–99.

Box HO, Gibson KR, eds. 1999. Mammalian Social Learning: Comparative and Ecological Perspectives. Cambridge (United Kingdom): Cambridge University Press.

Boyd R, Richerson PJ. 1985. Culture and the Evolutionary Process. Chicago: University of Chicago Press.

———. 1988. An evolutionary model of social learning: The effects of spatial and temporal variation. Pages 29–48 in Zentall TR, Galef BG Jr, eds. Social Learning: Psychological and Biological Perspectives. Hillsdale (NJ): Lawrence Erlbaum.

Brooks R. 1998. The importance of mate copying and cultural inheritance of mating preference. Trends in Ecology and Evolution 59: 45–46.

Brown C, Laland KN. 2003. Social learning in fishes: A review. Pages 280–288 in Brown C, Laland KN, Krause J, eds. Learning in Fishes: Why They Are Smarter Than You Think. Special edition of Fish and Fisheries, vol. 4.

Brown G. 2003. Learning about danger: Chemical alarm cues and local risk assessment in prey fishes. Fish and Fisheries 4: 227–234.

Chivers DP, Smith JF. 1994. Fathead minnows, *Pimephales promelas,* acquire predator recognition when alarm substance is associated with the sight of unfamiliar fish. Animal Behaviour 48: 597–605.

Chou LS, Richerson PJ. 1992. Multiple models in the social transmission of food selection by Norway rats, *Rattus norvegicus.* Animal Behaviour 44: 337–343.

Cook M, Mineka S. 1989. Observational conditioning of fear to fear-relevant and fear-irrelevant stimuli in rhesus monkeys. Journal of Abnormal Psychology 98: 448–459.

Coussi-Korbel S, Fragaszy DM. 1995. On the relationship between social dynamics and social learning. Animal Behaviour 50: 1441–1453.

Curio E. 1988. Cultural transmission of enemy recognition by birds. Pages 75–97 in Heyes CM, Galef BG Jr, eds. Social Learning in Animals: The Roots of Culture. San Diego: Academic Press.

Dautenhahn K, Nehaniv CL, eds. 2002. Imitation in Animals and Artifacts. Cambridge (MA): MIT Press.

Day RL, Coe RL, Kendal JR, Laland KN. 2003. Neophilia, innovation and social learning: A study of intergeneric differences in Callitrichid monkeys. Animal Behaviour 65: 559–571.

Dugatkin LA. 1992. Sexual selection and imitation: Females copy the mate choice of others. American Naturalist 139: 1384–1389.

Dugatkin LA, Godin J-G. 1993. Female mate-choice copying in the guppy (*Poecilia reticulata*): Age-dependent effects. Behavioral Ecology 4: 289–292.

Fragaszy DM, Perry S, eds. 2003. The Biology of Traditions: Models and Evidence. Cambridge (United Kingdom): Cambridge University Press.

Freeberg TM. 1996. Assortative mating in captive cowbirds is predicted by social experience. Animal Behaviour 52: 1129–1142.

———. 2004. Social transmission of courtship behavior and mating preference in brown-headed cowbirds, *Molothrus ader.* Learning and Behavior 32: 122–130.

Galef BG Jr. 1989. Enduring enhancement of rat's preferences for the palatable and the piquant. Appetite 13: 81–92.

———. 1992. The question of animal culture. Human Nature 3: 157–178.

Galef BG Jr, Clark MM. 1971. Parent–offspring interactions determine time and place of first ingestion of solid food by wild rat pups. Psychonomic Science 25: 15–16.

Galef BG Jr, Heiber L. 1976. The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. Journal of Comparative and Physiological Psychology 90: 727–739.

Galef BG Jr, Heyes CM. 2004. Social learning and imitation. Learning and Behavior 32: 1–140.

Galef BG Jr, Sherry DF. 1973. Mother's milk: A medium for the transmission of cues reflecting the flavor of mother's diet. Journal of Comparative and Physiological Psychology 83: 374–378.

Galef BG Jr, Whiskin EE. 2003. Socially transmitted food preferences can be used to study long-term memory in rats. Learning and Behavior 31: 160–164.

———. 2004. Effects of environmental stability and demonstrators' ages on Norway rats' social learning of food preferences. Animal Behaviour 68: 897–902.

Galef BG Jr, White DJ. 1998. Mate-choice copying in Japanese quail, *Coturnix coturnix japonica.* Animal Behaviour 55: 545–552.

Galef BG Jr, Wigmore SW. 1983. Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. Animal Behaviour 31: 748–758.

Galef BG Jr, Mason JR, Preti G, Bean NJ. 1988. Carbon disulfide: A semiochemical mediating socially-induced diet choice in rats. Physiology and Behavior 42: 119–124.

Galef BG Jr, Marczinski CA, Murray KA, Whiskin EE. 2001. Studies of food stealing by young Norway rats. Journal of Comparative Psychology 115: 16–21.

Giraldeau L-A, Beauchamp G. 1999. Food exploitation: Searching for the optimal joining strategy. Trends in Ecology and Evolution 14: 102–106.

Giraldeau L-A, Caraco T. 2000. Social Foraging Theory. Princeton (NJ): Princeton University Press.

Giraldeau L-A, Lefebvre L. 1987. Exchangeable producer and scrounger roles in a flock of feral pigeons: A case for the skill pool effect. Animal Behaviour 34: 797–803.

Hansell MH. 1984. Animal Architecture and Building Behaviour. New York: Longman.

Helfman GS, Schultz ET. 1984. Social transmission of behavioural traditions in a coral reef fish. Animal Behaviour 32: 379–384.

Hepper PG. 1988. Adaptive fetal learning: Prenatal exposure to garlic affects postnatal preference. Animal Behaviour 36: 935–936.

Heyes CM, Galef BG Jr, eds. 1996. Social Learning and Imitation: The Roots of Culture. New York: Academic Press.

Holldobler B, Wilson EO. 1994. Journey to the Ants: A Story of Scientific Exploration. London: Belknap Press.

Humle T, Matsuzawa T. 2002. Ant dipping among the chimpanzees of Bousou, Guinea and some comparisons with other sites. American Journal of Primatology 58: 133–148.

Hunt GR. 2000. Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides.* Proceedings: Biological Sciences 267: 403–413.

Hunt GR, Gray RD. 2002. Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proceedings: Biological Sciences 270: 867–874.

Kendal JR. 2002. An investigation into social learning: Mechanisms, diffusion dynamics, functions and evolutionary consequences. PhD dissertation. University of Cambridge, Cambridge, United Kingdom.

Kendal RL, Coolen I, van Bergen Y, Laland KN. Tradeoffs in the adaptive use of social and asocial learning. Advances in the Study of Behavior. Forthcoming.

Kenward B, Weir AAS, Rutz C, Kacelnik A. 2005. Tool manufacture by naive juvenile crows. Nature 433: 121.

Kirkpatrick M, Dugatkin LA. 1994. Sexual selection and the evolutionary effects of copying mate choice. Behavioral Ecology and Sociobiology 34: 443–449.

Laland KN. 1994. Sexual selection with a culturally transmitted mating preference. Theoretical Population Biology 45: 1–15.

———. 2004. Social learning strategies. Learning and Behavior 32: 4–14.

Laland KN, Plotkin HC. 1991. Excretory deposits surrounding food sites facilitate social learning of food preferences in Norway rats. Animal Behaviour 41: 997–1005.

Laland KN, Williams K. 1997. Shoaling generates social learning of foraging information in guppies. Animal Behaviour 53: 1161–1169.

———. 1998. Social transmission of maladaptive information in the guppy. Behavioral Ecology 9: 493–499.

Laland KN, Richerson PJ, Boyd R. 1993. Animal social learning: Toward a new theoretical approach. Perspectives in Ethology 10: 249–277.

Lefebvre L, Palameta B. 1988. Mechanisms, ecology, and population diffusion of socially learned, food-finding behavior in feral pigeons. Pages 141–164 in Zentall TR, Galef BG Jr, eds. Social Learning: Psychological and Biological Perspectives. Hillsdale (NJ): Lawrence Erlbaum.

Lupfer G, Frieman J, Coonfield D. 2003. Social transmission of flavor preferences in two species of hamster (*Mesocricetus auratus* and *Phodopus campbelli*). Journal of Comparative Psychology 117: 449–455.

McGrew WC. 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge (United Kingdom): Cambridge University Press.

Menzel EW. 1974. A group of young chimpanzees in a one-acre field. Pages 93–153 in Schrier AM, Stollnitz F, eds. Behavior of Non-human Primates: Modern Research Trends, vol 5. New York: Academic Press.

Mock DW, Lamey TC, Thompson DBA. 1988. Falsifiability and the information center hypothesis. Ornis Scandinavica 19: 231–248.

Nicol CJ, Pope SJ. 1999. The effects of demonstrator social status and prior foraging success on social learning in domestic hens. Animal Behaviour 57: 163–171.

Persaud KN, Galef BG Jr. 2005. Eggs of a female quail are more likely to be fertilized by a male that she prefers. Journal of Comparative Psychology. Forthcoming.

Schlag KH. 1998. Why imitate, and if so, how? A bounded rational approach to multi-armed bandits. Journal of Economic Theory 78: 130–156.

Smotherman WP. 1982. In utero chemosensory experience alters taste preferences and corticosterone responsiveness. Behavioral and Neural Biology 36: 61–68.

Steiniger F. 1950. Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. Zeitschrift für Tierpsychologie 7: 356–370.

Tebbich S, Taborsky M, Fessl B, Blumqvist D. 2001. Do woodpecker finches acquire tool use by social learning? Proceedings: Biological Sciences 268: 2189–2193.

Templeton JJ, Giraldeau L-A. 1996. Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. Behavioral Ecology and Sociobiology 38: 105–113.

Terkel J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). Pages 17–48 in Heyes CM, Galef BG Jr, eds. Social Learning in Animals: The Roots of Culture. San Diego: Academic Press.

Van Bergen Y, Coolen J, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proceedings: Biological Sciences 271: 957–962.

Ward P, Zahavi A. 1973. The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115: 517–534.

Warner RR. 1988. Traditionality of mating-site preferences in a coral reef fish. Nature 335: 719–721.

West MJ, King AP. 1980. Enriching cowbird song by social deprivation. Journal of Comparative Psychology 94: 263–270.

———. 1988. Female visual displays affect the development of male song in cowbirds. Nature 334: 244–246.

White DJ, Galef BG Jr. 2000a. "Culture" in quail: Social influences on mate choices of female *Coturnix japonica*. Animal Behaviour 59: 975–979.

———. 2000b. Differences between the sexes in direction and duration of response to seeing a potential sex partner mate with another. Animal Behaviour 59: 1235–1240.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 2001. Charting cultural variation in chimpanzees. Behaviour 138: 1481–1516.

Wilkinson GS. 1992. Communal nursing in evening bats. Behavioral Ecology and Sociobiology 31: 225–235.

Zentall TR, Galef BG Jr, eds. 1988. Social Learning: Psychological and Biological Perspectives. Hillsdale (NJ): Lawrence Erlbaum.