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## Introduction

The study of social learning sits at the interface of a truly astonishing number of academic disciplines. How many other fields could boast being central to both social anthropology and human evolution; core material for both experimental psychologists and theoretically minded economists; or emerging influences in the fields of both cognitive neuroscience and artificial intelligence?

The observation that many animals, including humans, acquire valuable life skills and knowledge through copying others has been the focus of attention of animal behaviorists dating back to Darwin. Likewise, social learning, the diffusion of innovations, conformity, and social influences on child development have been key concepts within the social sciences for over a century. However, in recent decades, the field of social learning has received such unprecedented attention spread across the sciences, social sciences, and humanities, and experienced such growth, that researchers within the field have referred to an “explosion of interest” in the topic (Galef and Giraldeau 2001; Shettleworth 2001). Long gone are the days when research on imitation could (ungenerously) be characterized as the esoteric province of an obscure branch of comparative psychology. Now, social learning is a rapidly growing subfield of animal cognition research; while biological anthropologists and archaeologists are constructing models of cultural evolution, economists are frequently talking norms and herding behavior, neuroscientists are mapping circuitry associated with social influences on decision making, and engineers are building imitating robots.

The diverse backgrounds of the researchers studying social learning contribute to the field’s controversies. East African but not West African chimpanzees use stalks to fish for termites, while western but not eastern chimps crack open nuts with stone hammers. Capuchin monkeys in Costa Rica exhibit extraordinary

social conventions, such as sniffing each other's hands and placing fingers in each other's mouths. Humpback whales and chaffinches sing different songs than their fellow conspecifics living in different regions. If these, and other, animal traditions are acquired through social learning, are behavioral scientists justified in speaking of animals possessing "culture"? Or are anthropologists correct to assert that human cultures are so imbued with meaning, so permeated with symbolism, and so reliant on uniquely human aspects of cognition, that to liken them to the behavioral traditions of animals is, frankly, ridiculous? Is human social learning shaped by evolved structure in the mind then biased to acquire content—from choosing sugar rich foods to admiring specific body shapes—that proved adaptive among our Pleistocene ancestors, as suggested by many evolutionary psychologists? Or is human learning dominated by general rules (e.g., copying the highest payoff behavior or conforming to the local norm) that are for the most part acquired independently of their content, as claimed by cultural evolutionists? Is imitation critically dependent on the ability to take another individual's perspective, to understand their goals, or on complex cognition? Are socially learned traditions constrained in order to be adaptive? Can cultural processes support a viable form of group selection? And so on, and so forth. The controversies are multiple, ripe, and engaging, enriched by the varied standpoints that characterize adjacent disciplines struggling to understand a common topic.

The disparate backgrounds of those drawn into the field have also contributed to the newly emerging methods that are appearing to address these challenges. Until recently, experimental studies of social learning were restricted to behavioral investigations, typically conducted in the laboratories of comparative or developmental psychologists, and focused on very specific questions, such as: "Can animals imitate?" or "Do children acquire violent dispositions from others?" Similarly, with the exception of some early experiments on birdsong learning, biologists' interest in social learning was pursued almost entirely through observations and recordings of the natural behavior of animals, largely by ethologists and primatologists.

In recent years, however, new methods have become available, considerably expanding the social learning researcher's toolbox. These include (i) experimental and statistical methods that allow researchers to categorize cases of social learning according to their underlying psychological processes and learning mechanisms; (ii) neuroscientific methods for identifying the brain structures, neural circuitry, and physiological processes underlying both social learning and social influences on decision making; (iii) mathematical and statistical methods for identifying social learning when it occurs in natural populations (or in naturalistic contexts in captivity); (iv) experimental and statistical methods to predict and explain when humans and other animals copy, from whom they learn ("social learning strategies"), and to also detect the strategies deployed; and (v) mathematical methods for predicting the pattern of diffusion of novel learned innovations, and for modeling cultural evolution and gene-culture coevolution. Finally, numerous and diverse tools and procedures are available for applying social learning methods outside of academia. These range from commercial hatcheries

training hatchery-reared fish to recognize predators and thereby enhance restocking efforts, to predicting the pattern of spread of technological innovations and identifying likely targets for uptake.

This book is designed to be a complete and accessible practical guide for the social learning researcher and their students, as well as for others whose interest in social learning is less central. As it currently stands, there is no single source that reviews the aforementioned conceptual and methodological developments, and the field's new theory and tools are to be found in a diverse collection of articles in academic journals. This book is first and foremost a monograph on social learning concepts and methods; it seeks to summarize and extend new developments in the field, rendering the new tools available to a broader constituency and heightening awareness of this emerging research topic. However, such is the growth of interest in social learning that we envisage the material contained in this book to be of interest to many individuals, academic and nonacademic, who are not directly connected to the immediate field. Social learning and imitation, including their mechanisms, methods, and models, have become central to a broad range of disciplines, and significant progress in their scientific understanding is potentially of widespread interest, both within and outside academia.

In order to discuss the conceptual foundations of social learning some definitions will be necessary from the outset. Certain terms, including “social learning,” “imitation,” “innovation,” “tradition,” and “culture,” will appear repeatedly throughout this book. In almost all cases, there exists no universally accepted definition, and in many instances the terms are the focus of considerable debate. Accordingly, at the outset we provide initial definitions for these labels, though later in the book we will suggest refinements. A summary of these definitions is given in box 1.1, with a justification presented below.

## 1.1 What Is Social Learning?

The most commonly used definition of social learning is “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (Heyes 1994); this draws on a similar earlier generic definition by Box (1984). This definition is extremely broad, and indeed might be regarded as problematically so. The concern here is that the phrase “influenced by” lacks specificity. To take matters to the extreme, the presence of another individual might even impede learning, yet would still meet the above definition, because the other's activities constitute an influence on learning. It is then perhaps not surprising that others have used the term “social learning” to refer to a more specific concept. For example, Lonsdorf and Bonnie (2010) restrict social learning to cases in which seeing another individual performing a behavior pattern causes the observer to learn the same pattern; this approximates our use of the term “social transmission.”

This ambiguity in the meaning of the term “social learning” has the potential to lead researchers into the logical error of equivocation, which occurs when the meaning of a term is changed during a line of reasoning. For example, those

### Box 1.1

#### Preliminary definitions

**Social learning** is learning that is facilitated by observation of, or interaction with, another individual or its products.

**Social transmission** occurs when the prior acquisition of a behavioral trait T by one individual A, when expressed either directly in the performance of T or in some other behavior associated with T, exerts a lasting positive causal influence on the rate at which another individual, B, acquires and/or performs T.

An **innovation** (sensu **product**) is a new or modified learned behavior not previously found in the population.

**Innovation** (sensu **process**) is a process that introduces novel behavioral variants into a population's repertoire and results in new or modified learned behavior.

A **tradition** is a distinctive behavior pattern shared by two or more individuals in a social unit that persists over time and that new practitioners acquire in part through socially aided learning.

**Cultures** are those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.

definitions of “culture” (see below) that emphasize geographic differences in behavior caused by social learning (e.g., Laland and Hoppitt 2003) typically have in mind a narrower conception of social learning, more akin to the Lonsdorf and Bonnie definition than the broader Heyes definition. There could be a danger that researchers might prematurely make the claim of culture if variant forms of social learning in the broader sense were identified for a given species. This is particularly problematic if different researchers interpret the term “social learning” with variant levels of breadth, unaware of discrepancies in usage.

On the face of it, a solution might be to adopt a narrower definition of social learning, with another term for the broader category; for example, “socially biased learning” could be used (e.g., Humle et al. 2009). However, there are two concerns here. First, the broad definition is widely used and accepted, and hence it may lead to further confusion if we to advocate a change in usage. Second and more importantly, narrower definitions could miss out on some phenomena of interest to those who would consider themselves social learning researchers. For example, a definition that requires matching behavior would not include cases where an observer learns what not to do, perhaps after watching another individual make a mistake. Consequently, on balance, we maintain that a broad and generic term still has some currency and propose the following definition, modified from Heyes (1994):

Social learning is learning that is facilitated by observation of, or interaction with, another individual (or its products).

Our use of the term “facilitated” restricts forms of social interaction that generate social learning to those that have a positive influence on the observer

learning. Instances where social interaction impedes learning are better captured by a different term, such as “social inhibition” (Brown and Laland 2002). Even with this refinement, the definition of social learning remains broad, meaning a researcher’s primary task is to investigate the manner in which learning is social, rather than to answer whether learning is social learning or not. This kind of reasoning justifies researchers’ tendency to focus on general social processes thought to be widely important in promoting social learning, potentially across different contexts and modalities, rather than on isolated or specialized instances.

Throughout this book we will refer to the individual who learns socially as the “observer” and the individual that they learn from as the “demonstrator.” While we acknowledge drawbacks to both of these terms, there are no obviously superior alternatives.<sup>1</sup>

## 1.2 Social Transmission

Notwithstanding the utility of a generic term, researchers clearly require more specific terms to describe different types of social learning. In recent years there has been a concerted effort to develop methods to “detect social learning” in natural populations (see chapters 5–7). Such methods are not really aimed at detecting social learning in the broad sense, but rather to detect what we term “social transmission.” This term was initially coined by Galef (1976), and subsequently described as “cases of social learning that result in increased homogeneity of behavior of interactants that extends beyond the period of their interaction” (Galef 1988, 13). Familiar examples include the spread of sweet potato washing in Japanese monkeys (Kawai 1965) and hybrid-corn use by American farmers (Ryan and Gross 1943). Our definition of social transmission is very much in the same spirit as Galef’s, but is designed to confer greater precision:

Social transmission occurs when the prior acquisition of a behavioral trait  $T$  by one individual  $A$ , when expressed either directly in the performance of  $T$  or in some other behavior associated with  $T$ , exerts a lasting positive causal influence on the rate at which another individual  $B$  acquires and/or performs  $T$ .<sup>2</sup>

<sup>1</sup> The term “observer” would mislead if it implied that social learning is solely reliant on vision; however, our usage is not constrained to any sensory modality. Likewise, “demonstrator” might imply the deliberate production of the target behavior, an implication that we do not wish to be drawn. In the majority of instances of animal social learning the “demonstrator” makes no attempt to transmit knowledge. In this regard, the term “model” is arguably preferable, being more neutral, but it brings with it the potential for confusion in discussions of mathematical and statistical models of social learning. A host of other terms (“actor,” “transmitter,” “receiver,” “source,” “sink,” “learner”) are used in the social learning literature but all suffer from drawbacks.

<sup>2</sup> This definition is adapted from Hoppitt, Boogert, and Laland (2010), in which we provided a definition of social transmission that also allowed “information” to be transmitted instead of a behavioral trait. In principle, the definition could be used for a piece of information, but in practice it might be difficult to detect unless the information is associated with an observable behavioral trait.

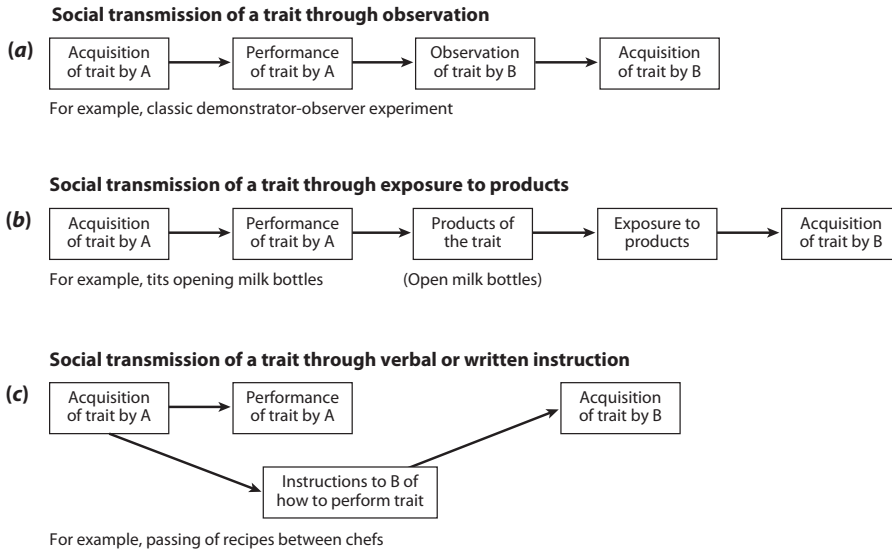
Here a behavioral trait is a target behavior pattern, which might be specific to a particular context (e.g., pigeons pecking at a lever in response to a green light; Dorrance and Zentall 2002). Inclusion of the phrase, “expressed either directly in the performance of  $T$  or in some other behavior associated with  $T$ ” is recognition of the fact that acquired information and behavior can be transmitted with or without performance of the trait. Examples of the latter are not uncommon. In the case of humans, for example, we can provide written or spoken instructions on how to perform the trait, instead of demonstrating it directly. For example, social transmission of a recipe between chefs might occur when one chef passes a recipe to another. The number of times a chef cooks the recipe might have no causal influence on the acquisition of the recipe by others, but we would still consider this social transmission (see fig. 1.1c). In the case of other animals, signals such as food calls (e.g., the vocalizations of callitrichid monkeys that recruit infants to a desirable or novel food source [Rapaport and Brown 2008], or mother hens that warn their chicks from consuming a toxic foods [Nicol and Pope 1996]) or the opportunity teaching exhibited by several carnivores (e.g., when meerkat helpers provision pups with disabled prey; Thornton and McAuliffe 2006) can facilitate social transmission without direct performance of the trait by a demonstrator.

We also recognize two types of social transmission, which we call social transmission of trait acquisition (where the effect of social transmission is on the rate at which  $B$  acquires  $T$ ) and social transmission of trait performance (where the effect is on the rate at which  $B$  performs  $T$ ). In practice, many cases are likely to involve both the social transmission of trait acquisition and of trait performance—where individuals who observe a demonstrator both acquire the trait sooner and perform it more frequently once they acquire it, than individuals who do not observe a demonstrator. Nonetheless, we see the two as logically distinct. Observers might acquire  $T$  sooner, but may not perform  $T$  any more frequently than individuals who have acquired it asocially.<sup>3</sup>

It might seem strange to some readers to discuss a rate at which acquisition of a trait occurs, when each individual can only acquire a trait once (except when an individual has forgotten a trait and then does learn it again). Here our use of the term “rate” is in the sense of a “hazard rate” in time to event or in “survival” models—comparable to the rate of death or the rate at which a machine component fails—which therefore refers to the pattern of learning spread across a sample of individuals.<sup>4</sup> For example, if a large sample of individuals all had a learning rate of 0.5 per hour, we would expect the mean time to acquisition to be  $1/0.5 = 2$  hours.

<sup>3</sup> When we use the term “asocial” in contrast to “social transmission,” we mean that it has not been socially transmitted; we do not mean that it has not been affected by any social cues.

<sup>4</sup> We suggest the rate at which individuals acquire a trait as the most general criterion. Note, were we instead to utilize the probability that another acquires the trait, this would not allow for the fact that individuals who are not influenced by informed individuals might also reliably acquire the trait, but tend to do so later. Nonetheless, rates can easily be converted into a probability of acquisition for a specified time period, so the probability of acquisition within an individual’s lifetime or an experimental trial can still be used to detect social transmission.



**Figure 1.1.** Three causal pathways through which information can be socially transmitted from individual *A* to individual *B*. An arrow represents a direct causal influence between two types of event (i.e., one that is not mediated through another type of event present in the graph). For example, in (a) if *B* observes *A* performing the trait, then *A*'s action must be a cause of *B* observing the trait. In this case, observation of the trait then causes *B* to acquire the trait. In (a) the causal influence of the performance of the trait by *A* on the acquisition of the trait by *B* is mediated entirely through observation, whereas in (b) it is mediated entirely through exposure to a product. In reality, both causal pathways might operate. See Shipley 2000 for an accessible introduction to causal graphs (see also chapter 6).

Our definition also covers the case in which there are two or more traits that are alternative variants for the same function, and (1) the variant possessed by *A* causes *B* to be more likely to acquire the same variant,<sup>5</sup> and/or (2) the preferences of *A* for one variant causes *B* to develop a similar preference. Definitions in terms of rates also have the advantage that they allow researchers to model trait acquisition or performance as a stochastic process, and thereby infer social transmission from relatively complex patterns of acquisition or performance (see chapter 5). As indicated above, we interpret the phrase “performance” broadly to encompass transmission mediated by an animal’s products, including, in the case of humans, signs, signals, and linguistic information.

There are clearly a number of causal routes by which a trait *T* could be socially transmitted between individuals *A* and *B*. Figure 1.1 illustrates three such cases. Perhaps the most obvious is social transmission through observation: *B* observing trait *T* being performed by *A*, causes *B* to acquire *T* (fig. 1.1a). It is this causal pathway that most traditional observer-demonstrator experiments aim to detect.

<sup>5</sup> For example, if each individual sticks with whichever variant it acquires first, the probability that it will acquire variant *a* rather than another variant, is  $p_a = \lambda_a / \sum_x \lambda_x$ , where  $\lambda_x$  is the rate of acquisition of variant *x*. Therefore, a positive causal influence on  $\lambda_a$  is also a positive causal influence on  $p_a$ .

There are also a number of documented cases where the physical products of the performance of  $T$  (excluding visual and auditory cues) can play a role in social transmission (fig. 1.1b). For example, Heyes and Dawson (1990) found that in rats the trait of pushing a joystick in a particular direction for a food reward was socially transmitted from trained demonstrators to observers, and that olfactory cues left on the joystick were sufficient for this effect to occur (Mitchell et al. 1999; see also Galef and Beck 1985; Laland and Plotkin 1991). Some researchers argue that social transmission mediated through physical traces left by animals in their environment is likely to be highly important in natural populations (Fragaszy, 2012b). We discuss several such examples in chapter 3.

It is also possible that both types of social transmission could operate indirectly through the behavior of an intermediate individual. A possible example of such transmission is provided by brown-headed cowbirds (*Molothrus ater*). Freeberg (1996, 1998) found that female cowbirds prefer to mate with males from the same cultural background, and that this preference seems to be based largely on the males' vocalizations. It has also been shown that females respond to preferred song types with the wing stroke display, which causes males to perform those song types more frequently (West and King 1988). This suggests the songs heard by a female during development cause her to respond to those types later by performing the wing stroke display. This in turn causes the males with which she interacts to perform those song types more. This would mean that song type performance is transmitted between males through the mating preferences of females, and mating preferences are transmitted between females through the singing of males.

Note also, we place emphasis on social transmission as a whole, rather than on a more specific subset of social learning, such as social transmission through direct observation. We do this because the term identifies with precision the subset of social learning that can result in the spread of a trait through a population of animals, in terms of either acquisition or frequency of performance. There is clearly some utility for a generic term for processes that can underpin such a diffusion.

An obvious experimental procedure for detecting social transmission in a laboratory setting is the traditional demonstrator-observer experiment, which we discuss in detail in chapters 3 and 4. Briefly, the experimenter exposes naïve observers to demonstrators performing the trait in question (for example, the solution to a foraging task), and compares the observers' rate of acquisition or performance with that of control subjects. The exact way in which the experiment is set up determines which types of social transmission can be detected—for example, if observers are not allowed access to the products of a demonstrator's behavior the experimenter will not detect the social transmission pathway depicted in figure 1.1b.

Historically, demonstrator-observer experiments have frequently sought to determine whether subjects have a capacity for a specific mechanism of social learning, such as imitation. In chapter 4 we discuss such mechanisms and describe how they can be distinguished. However, laboratory experiments do not



tell us how important social transmission is in natural settings where animals can freely interact; experiments have little to say about behavioral traits that arise naturally. In some cases it might be possible to set up comparable field experiments to elucidate the role of social transmission in development (see section 3.2 and chapter 8). In other cases, this might not be possible, and the researcher may be limited to inferring social transmission from the distribution of traits in individual or group repertoires, or from the pattern of spread of a behavioral trait. As always, the absence of experimental manipulation makes inferring causal pathways more difficult (Shipley 2000). In such cases the researcher will be limited to detecting statistical patterns that are consistent with social transmission, and that may also rule out any plausible alternative causal hypotheses. In recent years a number of candidate methods have arisen that attempt to accomplish this, which we discuss in chapters 5–7.

### 1.3 Imitation

In chapter 4 we discuss twelve processes through which a demonstrator can influence the behavior of an observer in a manner that increases the probability that the observer learns; these are listed with definitions in table 4.1. Two of these processes possess the word “imitation” in their name: “contextual imitation” (learning to use an established action in a novel context) and “production imitation” (the learning of a new motor pattern). Each constitutes a highly specific means through which the activities of one individual may trigger learning in another individual (see chapter 4 for more precise definitions). We are, of course, aware that the word “imitation” is used in a more generic sense in some academic fields, notably economics, where its use as an umbrella term to refer to all forms of social learning could be considered synonymous to our use of “social transmission.” Throughout this book, to avoid confusion, we restrict our use of the term “imitation” to the narrower meanings defined in chapter 4.

### 1.4 Innovation

The appearance of sweet potato washing in Japanese monkeys (Kawai 1965) and of hybrid-corn use by American farmers (Ryan and Gross 1943) are both also examples of “innovation”—the invention of new behavior patterns. Humans, of course, have devised literally millions of novel innovations, from computers to soufflé, to sonatas (Basalla 1988; E. Rogers 1995; Sternberg 1999; Simonton 1999), in many cases building on earlier inventions. There are also hundreds of innovations reported in animals, ranging from the incorporation of new items into foraging repertoires to novel elements in the songs of birds, to novel courtship displays, feeding behaviors, and tool use in primates (Byrne 1999; Casanova 2008; Lefebvre et al. 2004; Reader and Laland 2003a). Each of the many thousands of reports of social transmission in the animal behavior and human

diffusion of innovation literatures typically involve initiation by a single individual's invention. While at the mechanistic level, the consanguinity of animal and human innovation is a matter of debate, from a functional perspective, these phenomena exhibit clear similarities in humans and nonhumans (Reader and Laland 2003).

Reader and Laland (2003b) distinguished between *innovation sensu product*, which refers to the new idea or invention that is learned, and *innovation sensu process*, which is the inceptive process that led to the new product. Following these authors, throughout this book *an innovation (sensu product) is a new or modified learned behavior not previously found in the population*, while *innovation (sensu process) is a process that introduces novel behavioral variants into a population's repertoire and results in new or modified learned behavior*. This contrasts with some definitions of human innovation, which refer to acquisition of a novel act by any route as innovation, and the initial inception as "invention" (E. Rogers 1995).

Fragaszy and Perry (2003, xiii) defined a "tradition" as *a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning*. We interpret the phrase *persists over time* as meaning that to qualify as tradition the behavior must be maintained through repeated bouts of social transmission, such that each learner is then potentially capable of passing on the acquired information to others, thereby allowing the behavior to become characteristic of the population or of a subgroup within it. Whiten et al. (2011) note that "this makes sense insofar as a continuum is possible, from mere fads and fashions (perhaps lasting only weeks or even much less) to those that pass down very many generations"; they add that "particularly robust evidence of traditions comes from those that are of long duration, or rely on multiple transmission events, whether between generations or within them." We will be utilizing this term to refer to human traditions and the natural traditions of animals (e.g., the use of stone hammers to open nuts among Tai forest chimpanzees; Whiten et al. 1999). We will also use the term to refer to laboratory traditions, such as the consistent pathways through a maze taken by laboratory populations of guppies (Laland and Williams 1997), and humans (Reader et al. 2008), in spite of turnover in the populations' composition (Laland and Williams 1997).

The concept of "culture" is particularly tricky, because it has proven extremely difficult for social scientists to operationalize or derive a consensual definition (Kroeber and Kluckholm 1952; Durham 1991), and many social anthropologists seem to have given up on the notion of culture altogether (Kuper 2000; Bloch 2000). Conversely, biologists and students of animal behavior are giving unprecedented attention to the "culture" of other animals, and like it or not, the term is ever present in various literatures. Among behavioral scientists, some authors essentially equate "culture" with "tradition," and references to population-specific vertebrate traditions for singing particular songs, exhibiting specific feeding behavior, and the like as "cultural transmission" are common (e.g., Slater 1986). However, other authors apply more stringent criteria to the use of the term "culture," arguing that animal cases such as these might otherwise be too readily

assumed to be reliant on mechanisms homologous (that is, sharing evolutionary ancestry) with human culture, when they might really be merely analogous (dependent on different forms of social learning, for example) (Galef 1992). Perhaps not surprisingly, there is a trend for those with a more functionalist perspective to emphasize the functional continuity of animal tradition and human culture, and for those from a background of studying mechanisms to emphasize the mechanistic discontinuity.

Nonetheless, two important aspects of culture are relatively noncontentious. First, culture is built upon socially learned and transmitted information; “culture” does not apply to genetic information or to knowledge and skills that individuals acquire alone. Second, socially transmitted information can underpin group-typical behavior patterns, which may vary from one population to the next. Thus, culture helps to explain both continuity within groups and diversity among groups. These considerations led us to the following definition (Laland and Hoppitt 2003, 151): *Cultures are those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.* It will be apparent that we make no real distinction between tradition and culture, and we will use these terms interchangeably throughout the book. This stance is entirely pragmatic—being designed to foster exploration of the evolutionary roots of human culture (Laland and Hoppitt 2003)—and is obviously not intended to imply that the “culture” of chimpanzees or chaffinches is identical to that of humans. We envisage that all “cultural” species will have their own distinctive species-typical modes of communication, learning, and social interaction that render their culture unique. Nonetheless, these concepts of culture have properties in common, particularly at the functional level, which are of broad interest.

### 1.5 Why Study Social Learning?

Current interest in social learning draws from a number of pressing research challenges and controversies. First, attention partly derives from a more general interest among behaviorists and neuroscientists in cognitive neuroscience and cognition: that general interest sets out to understand the biological and psychological bases of cognitive processing, often using animal models. Imitation has long been regarded of interest because of the enduring challenge of explaining what is known as “the correspondence problem”—in essence, how the brain converts the perception of an observed act into an enacted body movement (Heyes 2009). The nature of the challenge is most apparent for perceptually opaque actions, such as imitating facial expressions. The discovery of mirror neurons—neural networks that are active during observation and execution of the same actions—has renewed this interest, in part by exciting a further debate as to whether or not mirror neurons can be viewed as a solution to the correspondence problem, and whether mirror neurons are best viewed as preexisting enablers of imitation or as a byproduct of social learning (Rizolatti and Craighero 2004; Heyes et al. 2009).

Second, interest in social learning is the product of vigorous debates among psychologists, including whether social and asocial learning are reliant on the same underlying processes, whether evidence for some forms of social learning (notably “imitation”) might be indicative of animals possessing complex psychological capabilities (Heyes 1994; Tomasello and Call 1997; Hurley and Chater 2005), and whether imitation is best accounted for by transformational or associative theories (Heyes and Ray 2000; Heyes 2009; chapter 4). Also of interest here is the debate over neonatal imitation and, more generally, the role that imitation plays in child development (Carpenter 2006; Meltzoff and Prinz 2002), both of which we introduce in the following chapter. Recent experiments also suggest that imitation may be linked to prosocial attitudes and behavior (Van Baaren et al. 2009), a finding that has stimulated some excitement.

Third, social learning is of interest to ethologists, behavioral ecologists, primatologists, and cetologists, amongst others, because it seems to allow animals both to make adaptive decisions and to learn about their environments efficiently (Lefebvre and Giraldeau 1996). However, it can also sometimes propagate arbitrary and even maladaptive variants, and generate spatial variation partially disconnected from ecological distributions (Laland et al. 2009). For example, bluehead wrasse mating sites cannot be predicted from knowledge of environmental resource distributions (Warner 1988, 1990); rather, removal and replacement experiments demonstrate that mating sites are maintained as traditions. Cultural processes, like gene-frequency clines, can generate geographical patterns in behavioral phenotypes. Examples include the languages of Micronesia, which exhibit a correlation between geographic and linguistic distance (Cavalli-Sforza and Wang 1986); and bird and whale vocalizations, which exhibit similar patterns (Catchpole and Slater 1995; van Schaik et al. 2003; Janik and Slater 1997). Another challenging feature of cultural transmission is that, although it typically propagates adaptive behavior, both theory and empirical data suggest that under restricted circumstances arbitrary and even maladaptive information can spread. Once again, this is well documented in humans (Richerson and Boyd 2005). One case is informational cascades, where individuals base behavioral decisions on prior decisions of others (Bikhchandani et al. 1992; Giraldeau et al. 2002).

Fourth, evolutionary biologists have recognized that social learning can affect evolutionary dynamics and equilibria, and are increasingly exploring cultural evolution mathematically (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Richerson and Boyd 2005) and through laboratory experiments (McElreath et al. 2005; Mesoudi and O’Brien 2008). This is most obvious in humans, and a great deal of mathematical theory has investigated gene-culture coevolution (Boyd and Richerson 1985; Laland et al. 2010; Richerson et al. 2010). By homogenizing behavior across a population, and by allowing rapid changes in behavior, cultural processes typically increase rates of evolutionary change, although a reduction in rates of change is also possible (Feldman and Laland 1996; Laland et al. 2010). In other animals, theoretical models of mate-choice copying reveal that learned preferences could plausibly coevolve with gene-based traits (Kirkpatrick and Dugatkin 1994; Laland 1994); models of birdsong suggest

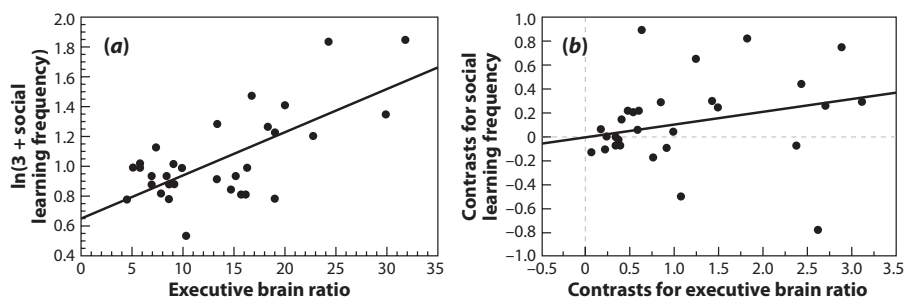
that song learning affects the selection of alleles influencing song acquisition and preference (Lachlan and Slater 1999); and other analyses have found that song learning could lead to the evolution of brood parasitism and facilitate speciation (Beltman et al. 2003, 2004).

Fifth, as described in chapter 2 and discussed again in subsequent chapters, biologists, psychologists, and anthropologists are engaged in a lively debate over the parallels and differences between animal traditions and human culture. These have been fueled by high-profile reports (*Nature*, *Science*, *PNAS*) of inter- and intrapopulation variation in the behavioral repertoires of animal populations, and claims of “culture” in apes (Whiten et al. 2005; van Schaik et al. 2003), monkeys (Perry et al. 2003), and cetaceans (Rendell and Whitehead 2001; Krützen et al. 2005).

Sixth, researchers studying robotics and artificial intelligence are paying attention to animal social learning as part of endeavors to develop “imitating robots” and related technology (Dautenhahn and Nehaniv 2002; Acosta-Calderon and Hu 2004). Part of the technological challenge in delivering imitating robots relates to the specification of what should and what should not be imitated by machines, without detracting from the flexibility that such machines are designed to confer. These sorts of insights are emerging from social learning studies in animals and humans.

Seventh, economists are increasingly interested in what they term “imitation,” specifically in whom one imitates, because it allows individuals to economize on computational costs, cash in on superior information, and increase learning efficiency (Schlag 1998; Apesteguia et al. 2003, 2005; Benhabib et al. 2011a, 2011b). There is agreement that social learning can influence economic decision making, and that a better understanding of such decision making is central to economics, business, and commerce. Moreover, there is widespread current interest in the processes that underlie cooperative behavior in humans, and one of the most prevalent theories emphasizes the role of strong reciprocity, which includes a conformist social learning element (Fehr and Fischbacher 2003). Moreover, the recent global financial crisis has stimulated interest in “herding” in financial institutions (Guarino and Cipriani 2008; Raafat et al. 2009), and in how social influences on individual decision making can sometimes trigger information cascades (Bikhchandani et al. 1992; Cao et al. 2011).

Finally, an eighth reason for the interest in social learning is that researchers from diverse backgrounds have been intrigued by the idea that it might play an important role in driving brain evolution and intelligence (Wyles et al. 1983; Wilson 1985; Boyd and Richerson 1985; Reader and Laland 2002; Whiten and van Schaik 2007; Reader et al. 2011; van Schaik and Burkart 2011; van Schaik et al. 2012). Allan Wilson (1985, 1991) suggested that through social learning individuals expose themselves to novel environmental conditions, which increases the rate of genetic change. He argued that the ability to invent new behavior and to copy the good ideas of others would give individuals an advantage in the struggle to survive and reproduce, and assuming that these abilities had some basis in neural substrate, this would generate selection for brain expansion. Boyd and Richerson (1985) view human cognition as having evolved to be specifically



**Figure 1.2.** Social learning covaries with brain size across primates. Based on figure 1 in Reader and Laland (2002).

adapted to the acquisition of cultural knowledge, a view now termed the “cultural intelligence” hypothesis and supported by a comparative analysis (Herrmann et al. 2007). A related hypothesis argues that evolved changes in the reliance on social learning favored the evolution of enhancements in other cognitive capacities, such as individual learning (Whiten and van Schaik 2007; van Schaik and Burkart 2011).

Consistent with this cluster of related ideas, it has been found that across primates, a species’ degree of reliance on social learning covaries strongly with measures of brain size (Reader and Laland 2002; see fig. 1.2). However, several other factors, ranging from social group size to diet (Clutton-Brock and Harvey 1980; Dunbar 1995; Deaner et al. 2000; Barton 2006), also correlate positively with primate brain volumes; this implies that the observed relationship between social learning and brain evolution may not be the result of a direct causal pathway between the two. Reader et al. (2011) provide a simple resolution to this paradox by showing that a large number of cognitive measures covary strongly across primates, suggesting that social, cognitive, and ecological capabilities may have coevolved. Social learning, tool use, and behavioral innovation form part of a correlated composite of cognitive traits evocative of general intelligence. This composite of traits covaries with species’ performance in laboratory tests of learning and cognition, as well as with brain volume measures. The analysis suggests that high levels of general intelligence evolved independently at least four times in primates, with independent responses to selection in capuchin, baboon, macaque, and ape lineages. It is striking that these are precisely the groups renowned for their social learning and traditions.

## 1.6 Summary of the Book

This book is designed to provide a practical guide for the social learning researcher, as well as a variety of useful tools, methods, concepts, and analyses for individuals in adjacent fields. In chapter 1, we have introduced the field of social learning research and presented the key ideas and concepts. Chapter 2 will provide a précis

of the history of interest in this topic. Chapter 3 describes research methods for investigating social learning in the laboratory, presenting traditional social learning experimental designs, transmission chain approaches, and controlled diffusion studies. It also draws attention to some recent neuroscientific analyses of social learning, which extend the study of social learning beyond the behavioral level. Chapter 4 presents a classification of social learning mechanisms, building on our earlier framework (Hoppitt and Laland 2008a), but extending the scheme to incorporate teaching. The chapter also describes how these mechanisms can be distinguished empirically. Chapters 5 to 7 depict methods for detecting and characterizing social learning in natural contexts, such as in the wild, or in natural social groups in captivity. Chapter 5 concentrates on diffusion methods, which endeavor to isolate social learning through characteristic signatures of socially mediated spread, such as network-based diffusion analysis. Chapter 6 describes repertoire-based methods for inferring social learning. These rely on the distribution of traits among individuals to ascertain whether social learning might account for behavioral differences within and among groups. Chapter 7 describes field experiments and developmental studies that provide additional means for identifying where social learning has occurred. Chapter 8 discusses social learning strategies—functional rules specifying what, when, and who to copy. As well as presenting the evidence for some of the better-studied learning heuristics, the chapter describes statistical procedures for identifying which social learning strategies are being deployed in a data set. Chapter 9 introduces a variety of diverse approaches to modeling social learning, cultural evolution, and gene-culture coevolution, including population-genetic, game-theoretical, agent-based, and spatially explicit models. Finally, in chapter 10 we end with a brief summary of which methods to apply in what circumstances.