

What Is Comparative Cognition About?

Comparative cognition is the study of cognitive processes in all species of animals, humans included. In this book, *cognition* embraces all processes involved in acquiring, storing, and using information from the environment, from perception to decision making, from a mouse's memory for familiar odors to a chimpanzee's apparently planful use of tools. The term *comparative* implies explicit comparisons of two or more species, but much comparative cognition research might be called the study of *animal cognition* because it focuses on just one non-human species or another. The goal of such research may be to compare the findings to those known from humans or to understand how particular species find their way around, choose food or mates, or the like. Either way, it contributes to the bigger picture of understanding the "endless minds most beautiful" (Finlay, 2007) of the other creatures on this planet, what they share and how they are unique, how and why they might have evolved.

From prehistoric times, interactions with other animals as prey, predators, or subjects of domestication have provided practical reasons for people to be interested in their minds and behavior. Practical considerations still motivate some research on animal cognition, such as that addressing issues in conservation and animal welfare. For instance, on some views how we treat animals in captivity should be determined by how closely their cognitive abilities resemble ours (see Dawkins, 2006). And much contemporary animal cognition research has the practical goal of developing "animal models" of human cognitive processes for use in investigating their neurobiological or genetic basis. This approach has

been especially successful in the study of memory (Chapter 2). But an equally important impetus for studying comparative cognition is sheer scientific curiosity. How *do* wood thrushes find their way from Pennsylvania to Central America in the fall and back again the next spring to the very same territory they occupied the year before? What does a baboon know about the complex social relationships among the other members of her troop, and how did she come to know it? What does her understanding of her social companions have in common with our understanding of our fellow human beings?

As the foregoing examples suggest, contemporary research on comparative cognition is multidisciplinary, with contributions not only from experimental psychologists but from biologists working in both laboratory and field, anthropologists, neurobiologists, and philosophers, among others. This makes for a lively and multifaceted research enterprise but also for the kinds of debate and disagreement that inevitably arise when people with different backgrounds and approaches try to communicate with one another. What unifies this diverse field is the overarching question with which the modern study of comparative cognition began, how true is Darwin's (1871) assertion that humans' "mental powers" are "different in degree but not in kind" from those of other species? For the first century or so after Darwin, students of comparative cognition were primarily concerned with documenting shared "mental powers," that is, cognitive processes, by looking for similarities between other animals and humans and by developing species-general theories of animal learning, memory, categorization, spatial representation, and the like. More recently the explosion of research on natural social groups of monkeys, apes, and other species has increased interest in social cognitive processes such as those involved in social learning and communication. Information from all these quarters has prompted reevaluation of Darwin's claim: although other species share many cognitive processes with us, a few may be uniquely human.

"From Darwin to Behaviorism": A Little History

In *The Origin of Species*, Darwin (1859) largely steered clear of the touchy topic of human evolution, but it was front and center in *The Descent of Man and Selection in Relation to Sex* (Darwin, 1871). The physical similarities between humans and apes might persuade some that they had evolved from a common ancestor, but evidence of mental similarity would be far more convincing. Accordingly, Chapters 2 and 3 of *The Descent of Man* marshaled

evidence to show "... that there is no fundamental difference between man and the higher mammals in their mental faculties" (Darwin, 1871, p. 35). Darwin claimed that other animals share with humans memory, attention, imitation, reasoning, even imagination and aesthetic and moral sensibility. His primary evidence was *anecdotal*, that is, opportunistic observations made by him or reported by others that seemed consistent with some "mental power" or another. For instance, the fact that his dog came out of the barn and greeted Darwin when he arrived home from his five-year voyage on the *Beagle* was evidence that animals have very good memory. Although some of Darwin's arguments were more speculative, he recognized that we cannot easily draw conclusions about conscious processes such as abstraction and self-consciousness in animals. "This difficulty arises from the impossibility of judging what passes through the mind of an animal; and again the fact that writers differ to a great extent in the meaning which they attribute to ... terms" (Darwin, 1879/2004, p. 105).

Darwin's writings inspired some of his supporters to seek further evidence for humanlike mental powers in nonhuman species. Primary among them was George Romanes (e.g. 1892), who could be less cautious than Darwin about interpreting anecdotes *anthropomorphically*, that is, by attributing humanlike behavior by an animal to humanlike thought and reasoning. For example, he suggested a cat that learned to open a gate must have seen people do it and reasoned, "If a hand can do it, why not a paw?" But such interpretations demand experimental tests, and around the beginning of the twentieth century relevant experiments began to appear, especially in the work of the American psychologist E. L. Thorndike (1911/1970). He placed cats and chicks in "puzzle boxes" from which they could escape by pulling strings, pushing levers, or the like. The animals showed no evidence of insightfully solving the problems but rather gradually became quicker to escape, learning by trial and error to perform the action that opened the box. Thorndike also found no evidence that any of the animals he tested could imitate a successful action performed by others of their species. For example, in a maze with two routes to food, chicks did not always follow the route they had seen a trained chick take.

The logic of Thorndike's simple test of imitation is fundamental to research on animal cognition (Heyes, 2008). Anthropomorphic interpretation of anecdotes like Romanes's story of the cat, that is, *folk psychology* (our everyday intuitive understanding of human psychology), suggests that animals should learn by copying others. But no matter how plausible the proposed explanation of a single observation or set of observations, there are nearly always other equally plausible explanations. In this case,

Thorndike's puzzle box data show that animals can learn gradually from the results of their own actions. The key then is to devise a situation in which the alternatives predict different outcomes. Here if chicks can imitate, the majority of them should follow the same route as the trained chick, whereas if they do not imitate in this situation but must learn where to go by individual trial and error, naive chicks will select the routes about 50:50 at first and about half of them will end up preferring each one. Unlike with purveying anecdotes, the goal of experiments such as these is not just to confirm that animals are (or are not) capable of doing something "clever" but to discover *how* they do what they do.

In experimental psychology, anthropomorphic interpretation of animal behavior along with the study of human subjective experience was largely eclipsed during the first two-thirds of the twentieth century by the development of behaviorism, which focused on observable behavior and eschewed explanation in terms of cognitive or other internal factors (Boakes, 1984). In research with animals, this approach reached its apotheosis with the work of B.F. Skinner and his followers, who studied the control of behavior by factors in the environment such as the stimuli present and the past schedule of reinforcement (reward and punishment). At more or less the same time in Europe, Konrad Lorenz, Niko Tinbergen, and their students, influenced by the Americans Craig and Whitman (see Burkhardt, 2005), developed the biological science of animal behavior, *ethology*. Ethology was distinct from psychology in that it embraced natural behavior of all kinds of animals. Ethologists worked primarily in the field studying behaviors such as mating, parenting, or foraging in insects, fish, and birds. But the ethologists' approach to behavior was as scrupulously objective as that of the Skinnerians. "Causal analysis" of behavior meant defining the current external stimuli and internal motivational conditions that, for example, caused a herring gull to roll an egg into its nest or a male stickleback fish to display courtship movements to a female (Burkhardt, 2005). But such analysis of *proximal* (i.e., immediate) *causes* was recognized as addressing only one of four questions that could be asked about behavior (Tinbergen, 1963). "Tinbergen's four questions" also include "How does behavior develop in the individual?" "How does it function in the animal's life, for example, in getting mates or reducing predation?" and "How did it evolve?" Although these questions are distinct, in ethology a complete understanding of any behavior includes answers to all of them (see Bolhuis & Verhulst, 2009).

The rigorous descriptions of behavior and relevant environmental stimuli characteristic of ethology and behaviorist psychology remain essential tools, but the latter part of the twentieth century saw major

changes in the central theoretical questions about animal behavior being asked by both psychologists and biologists. In the early 1970s in experimental psychology, the success of the "cognitive revolution" in the study of human minds stimulated parallel studies of animal cognition (e.g., Hulse, Fowler, & Honig, 1978). Often this meant studying familiar laboratory animals such as rats and pigeons in familiar learning tasks, but now behavior was not the object of study in itself but a window into internal, cognitive processes such as memory and representation. For instance, a well-known phenomenon from Skinnerian studies was the "scaloped" pattern of responding on fixed-interval (FI) schedules of reinforcement. When reward is given at regular intervals of time for, say, pecking or pressing a lever, animals perform the rewarded response very little immediately after each reward but more and more as the time for the next reward approaches. To someone interested in deducing cognitive processes underlying behavior, scalloping suggests the animal is not simply responding for as long as it takes to get food but timing the intervals between feedings. This intuition is supported by the observation that when food is occasionally withheld, responding declines in a predictable way after the usual time of food delivery. Models of the internal clock or interval timing mechanism were proposed and tested by, for example, varying the interval to be timed and measuring how precisely different durations could be discriminated (Chapter 3).

Meanwhile the biological study of animal behavior was seeing the development of *behavioral ecology*, which uses mathematical models to address Tinbergen's questions about evolution and current function. Such models are based on the assumption that behavior will evolve which increases *fitness*, the representation of the individual's genes in the next generation. Thus, it should optimize achievement of short-term goals that contribute to fitness such as rate of food intake or encounter with mates. Behavioral ecologists' models of optimal behavior during foraging and other activities were initially developed and tested without much regard for the cognitive or other proximal mechanisms necessary for their predictions to be fulfilled. This approach was and continues to be very successful (Westneat & Fox, 2010), but it soon became apparent that deviations from functional predictions could often be understood in terms of cognitive constraints. For example, modeling the best "patch" of the environment to forage in involves taking into account the amount of energy provided by the food items in each patch, how long it takes to find each one, and the time required to travel between patches. Animals seem to need a great deal of precise information for behavior

to fit the model perfectly, but they do not always have it. Perception of item quality inevitably has some error, learning may be incomplete, and memory is not always accurate. Such considerations, combined with the fact that tests of optimality models often had much in common with psychological studies of learning and choice, led to a more balanced approach, sometimes referred to as *cognitive ecology* (Dukas & Rattcliffe, 2009), in which studies of cognitive mechanisms are integrated with functional and evolutionary considerations, as discussed further in Chapter 3.

In the 1970s the biological study of animal behavior also saw the development of *cognitive ethology* in the writings of the distinguished biologist Donald Griffin (1978). Flying in the face of Tinbergen's (1951) injunctions against studying the unobservable processes of animal consciousness, Griffin claimed that the behaviorist approach denies important facts about animal behavior which ethologists should be trying to discover. He proposed frankly anthropomorphic explanations of all sorts of behaviors of all sorts of animals in terms of conscious thought and reasoning. For example, when a honeybee returns from a successful foraging trip and dances in the hive, she may be aware that she is telling other bees where the food is and want them to find it. As we see in Chapter 4, such questions have guided some important research on animal communication, but the results are not usually interpreted in terms of conscious awareness. Moreover, although Griffin's suggestions conflate the study of cognition with the study of consciousness, these are not necessarily the same. In everyday language we distinguish between merely responding to events and being conscious of them. Here *consciousness* refers to perceptual awareness, which can be distinguished from reflective consciousness, as might be shown in making a plan or deciding how well one knows the material for tomorrow's exam. Most people who study animal behavior, and others as well, would probably agree that animals have some form of perceptual awareness, but many question their possession of reflective or self-reflective consciousness (Dawkins, 2006). A related issue discussed in Chapter 5, but without implications for consciousness, is whether animals are capable of only first-order representations of events or whether some have higher order representations (Penn, Holyoak, & Povinelli, 2008). First-order representations are based on purely perceptual features of events, such as "he is making a fist" or "the tomato is red." Second-order representations involve abstractions from first-order properties: "he *feels angry*" or "the tomato is *the same color as the strawberry*."

In any case, most contemporary students of comparative cognition eschew discussion of the tricky subject of animal consciousness. Processes such as memory and attention are defined in terms of observable behaviors, what the animal does, not how it feels while doing it. This is true even when tackling questions suggested by our own introspection, such as bees' understanding of other bees' need to know. Pinning down humanlike cognitive processes in other animals means looking for *functional similarity* of behaviors across species. As a simple example, we might test a person's recognition memory by asking her, "Did you see this word earlier?" whereas we might test a mouse's recognition memory by training it to choose the one odor out of two that it encountered more recently. We could then vary factors known to affect human memory to see whether the mouse's performance changes as expected for a measure of memory. For instance, the longer the time since exposure to the to-be-remembered odor, the fewer correct choices the mouse should make. In the more challenging investigation of Griffin's suggestion about the bees, we would need to specify what behavior is evidence of sensitivity to another bee's need to know. The logic of functional similarity is a basic tool in comparative cognition research (Heyes, 2008), even though, as in the case of the honeybees, deciding what constitutes functional similarity between observable animal behavior and evidence of some interesting human cognitive process is not always straightforward or uncontroversial.

Research in the Twenty-First Century: Tool-Using Crows

An instructive example of contemporary research integrating the multiple approaches to comparative cognition is the study of tool use by New Caledonian crows. New Caledonian crows are a species of corvid (the bird family that also includes ravens, jays, and nutcrackers) found on the islands of the New Caledonian archipelago, a thousand miles or so east of Australia. Several populations of these crows use sticklike tools during foraging, mainly to extract prey from logs and crevices (Fig. 1.1). They make some of the tools they use, among other ways by nibbling off the stiff ribs of *Pandanus* palm leaves and shaping the edge into hook- or wedge-like structures (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007; Hunt, 1996). The shapes of tools differ in different parts of New Caledonia, suggesting that specific tool-making techniques are transmitted socially from one generation to another, making crow tool manufacture a candidate for animal culture (Holzhaider, Hunt, & Gray, 2010).

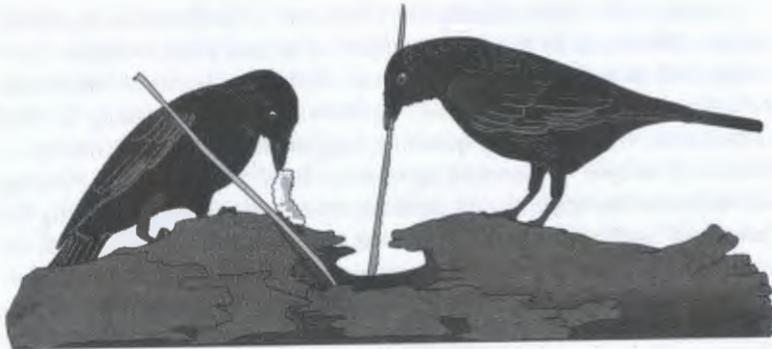


FIGURE 1.1. New Caledonian crows using stick tools. After a video frame with permission of Gavin Hunt and the University of Auckland.

Tool use by any animal attracts attention because this skill has traditionally been thought to be uniquely human, or at least the privilege of species such as chimpanzees that are closely related to humans. However, it turns out that animals from many widely separated branches of the evolutionary tree use tools (Chapter 3 and Bentley-Condit & Smith, 2010). Even among primates, tool use is not entirely predicted by relatedness to humans (Fig. 1.2). For example, the most widespread use of the greatest variety of tools is documented for chimpanzees, but bonobos (about as closely related to humans) do not seem to use tools very much in the wild, whereas orangutans (less closely related) do. Because birds are not closely related to humans, the apparently routine use and manufacture of tools by New Caledonian crows is even more compelling evidence that some special ecological conditions rather than a humanlike brain are key to evolution of tool use. What these conditions might be is suggested by the only other similar bird tool user, the woodpecker finch of the Galapagos Islands. Woodpecker finches use twigs and cactus spines to extract food from holes and crevices. They are not corvids nor their especially close relatives, but like New Caledonian crows they evolved on islands with no competing species such as woodpeckers that could harvest the same resources more efficiently.

In terms of evolutionary biology, tool use by chimpanzees and other apes is shared with human tool use by *homology*, or descent from a comparatively recent common ancestor that is assumed to have been a tool

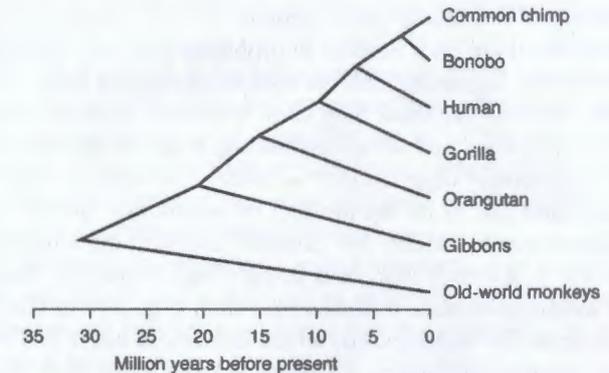


FIGURE 1.2. Evolutionary relatedness (phylogenetic tree) of the four great ape species, humans, gibbons (lesser apes), and old-world monkeys. Further explanation in the text. Adapted from Ernard & Pääbo (2004) with permission.

user. Similarity in species' DNA and known rates of random mutation are used to make inferences about evolutionary relatedness, as illustrated in Figure 1.2 by the *phylogenetic* (or evolutionary) *tree* for humans, great apes (chimpanzees, bonobos, gorillas, and orangutans), lesser apes (gibbons), and old-world monkeys. The nodes (points at sharp angles) show when, in million years before the present, groups or individual species diverged from inferred common ancestors. For example, the last ancestor bonobos and chimpanzees have in common with humans is thought to have lived about six million years ago. All three species have evolved since then from an unknown common ancestor that was neither a chimpanzee nor a modern human. Chimpanzees and bonobos began to evolve as distinct species even more recently. Because the last ancestor shared by birds and primates was some much more ancient primitive vertebrate that presumably did not use tools, bird tool use represents separate or *convergent* evolution in unrelated species as a consequence of common ecological conditions. The crows' tool use is *analogous* to human tool use, whereas that of apes is *homologous*. This distinction matters for discussions of cognitive evolution because analogous behaviors are probably less likely than homologous ones to be mediated by the same mechanisms.

Of course, tool use was thought to be uniquely human (or at least uniquely primate) in the first place because it seems to reflect high intelligence—inventiveness, understanding of physical principles, a large

brain, perhaps the ability to teach complex skills to others and to learn from them. But there are a number of problems with this anthropomorphic assumption, beginning with the idea of intelligence itself as applied to animals. Most people think they know what they mean by *intelligence* in everyday language; such an understanding is part of our folk psychology. But surprisingly often animal behaviors that appear intelligent at first glance turn out to be the product of remarkably “stupid” mechanisms (Shettleworth, 2010b). For example, a desert ant wandering out from its nest in search of food runs straight back home even from hundreds of meters away once it finds a prey item (Fig. 3.1c in Chapter 3). The ant looks as if it knows exactly where its home is, but in fact it knows only what distance and direction it needs to travel to get there. Place the ant with its food down somewhere else before the homeward trip and it runs in the same direction and for the same distance, then starts circling around as if expecting to find the nest. An ant wandering across the featureless desert has little spatial information other than distances and directions. It encodes these with great precision (Chapter 3), but the simple experiment just described reveals that it uses only the information it needs under normal conditions. Whether we want to describe it as intelligent or not is beside the point when it comes to analyzing the mechanisms underlying its behavior. We might want to say that “intelligence” is behavior that promotes survival and reproduction, that is, fitness, in natural conditions for the species, but this would render the term almost meaningless. We might also note that a person trying to perform like the ant on an appropriate relative spatial scale might fail miserably.

Besides highlighting the *anthropocentrism* (i.e., human-centeredness) in applying *intelligence* to animal behavior, the homing of the desert ant underlines a second point: *intelligence* in humans implies the general overall ability supposedly measured by IQ tests, whereas cognition in animals (and to some extent in humans) is *modular*. *Modularity*, the property of being made up of somewhat self-contained and independently functioning parts, is almost the rule when it comes to biological structures, but in the cognitive sciences the suggestion that human cognition is modular has been surprisingly controversial (see Barrett & Kurzban, 2006). However, other species provide plenty of evidence for a modular organization of cognition, with distinct abilities for distinct domains of information that have distinct abstract computational requirements. The desert ant is a superb navigator, but it doesn’t use tools. It computes the distance it travels over the ground by implicitly counting steps (Wittlinger, Wehner, & Wolf, 2007), but it probably cannot enumerate arbitrary items as monkeys do

(Chapter 3). As another example, Clark’s nutcrackers store thousands of pine seeds for the winter and have the excellent spatial memory required for retrieving them, but in laboratory tasks nutcrackers remember colors no better than other corvids and are worse than more social corvids at remembering the locations of items they saw other birds store (Balda & Kamil, 2006). That is, desert ants or Clark’s nutcrackers are not exceptionally “intelligent” in general, just especially good at specific skills that are important for their survival and reproduction.

The nutcracker’s exceptional spatial memory is an example of an *adaptive specialization* of cognition, an ability (spatial memory) shared across species but tweaked in each one in a way appropriate to its way of life. Physical structures and sensory systems (Chapter 2) provide many examples of adaptive specialization of shared characters. For instance, all birds have beaks but their shapes vary according to how they feed—tearing meat, cracking seeds, digging for worms, probing for nectar, and so on. Specific beak shapes are referred to as *adaptive* because they are assumed to have evolved as individuals with approximations to them experienced increased fitness compared to *conspecifics* (others of the same species) with other kinds of beaks. Of course, specialized structures are often accompanied by specializations in behavior and cognition. For instance, a hawk-like beak goes along with excellent stereoscopic vision and the ability to catch fast-moving prey. Cognitive adaptations would be expected to be reflected in neural specializations. An example in food-storing birds such as nutcrackers is correlation of the size of the hippocampus, a structure important for spatial memory in birds and mammals, with dependence on storing and retrieving food (Sherry, 2006).

It is rarely possible to prove hypotheses about adaptations because evolution proceeds so slowly, but evolutionary biologists have several kinds of evidence for them. These include comparing closely related species to see whether they differ in ways appropriate to differences in the environments they inhabit and observing how well present-day structures and behaviors work. The fact that animal species differ in cognitive specializations supports a modular analysis of cognition. But modular organization need not preclude some processes common to or cutting across domains (Barrett & Kurzban, 2006; Jeffery, 2010; West-Eberhard, 2003). These include perception, memory, and the simple forms of learning discussed in Chapter 2. In any case, evidence for modularity in animal cognition undermines the assumption that animals have some sort of general intelligence analogous to human IQ (but see Matzel & Kolata, 2010).

Returning to the New Caledonian crows, folk psychology suggests that when we call an animal tool-user intelligent we mean the animal understands what it is doing or knows how the tool works. New Caledonian crows certainly look as if they are doing more than performing a learned behavior describable as “insert a stick, wiggle it around, pull out a grub.” Understanding tools implies the ability to use them flexibly as the situation requires. This assumption has led to a variety of tests of what tool-using animals understand (Chapter 3). In one used first with monkeys, the animal can get a piece of food out of a long transparent horizontal tube by pushing or pulling on it with a stick. Once animals are proficient at this task, a “trap” is introduced in the middle of the tube: food directed toward it falls in and is lost (see Fig. 3.7 in Chapter 3). An animal that understands what the stick tool is doing has to notice the location of the food relative to the trap and insert the stick so as to move the food away from it. “Understanding” suggests animals should choose the correct end right away. Instead, however, all animals tested so far, both birds and primates, choose randomly at first and learn to choose correctly—sometimes surprisingly slowly—indicating that trial and error is required.

The trap tube test opposes anthropomorphic predictions to an alternative, here trial-and-error learning. The theoretical bias in the field of comparative cognition is very strongly toward explaining behavior in terms of such basic species-general mechanisms rather than invoking processes like reasoning or understanding. This bias is the expression of a principle known as *Lloyd Morgan's Canon*, stated by the early comparative psychologist Conwy Lloyd Morgan (1894, p. 53): “In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale.”

The Canon has plenty of problems (Sober, 2005). For instance, how do we judge “high” and “low”? The assumption that there is a “psychological scale” seems to reflect belief in a single *phylogenetic scale* of species, in which, for example, primates are more highly evolved than rats, which are higher than birds, which are higher than fish, which are higher than worms, and so on. The phylogenetic scale erroneously assumes linear progress in evolution rather than a Darwinian branching tree like that in Figure 1.2. A reasonable modern interpretation of Morgan's Canon is that explanations in terms of general processes of learning along with species-typical perceptual and response biases should always be sought before invoking more complex or specialized

cognitive processes. This stance is justified by the fact that the simple forms of learning such as habituation and classical conditioning discussed in Chapter 2 are very widespread in the animal kingdom, having been found in all species tested, including fruit flies and nematode worms (Papini, 2008). They may reflect ancient adaptations of neural circuits to universal causal regularities in the world. Because it is a good bet that any new species we study shares the capability for these forms of learning, the burden of proof is on anyone proposing that some novel, additional, cognitive mechanism has arisen on a particular branch of the evolutionary tree.

As for the New Caledonian crows, one might ask, if their tool using behavior is the result of trial-and-error learning, why don't more species of birds regularly use tools? The “why” in this question has answers in each of Tinbergen's four senses. We have seen a hint of the answer to the evolutionary “why” in special conditions on islands. The functional “why” could be addressed by determining the importance of foods obtained with tools in the crows' diet in the field (see Bluff et al., 2007). And as we have seen, tests of the underlying cognitive mechanisms suggest that the proximate causes do not include a specialized kind of physical understanding and therefore may be shared by many species. That leaves the question of how tool use develops, a question addressed by hatching and raising four New Caledonian crows in a lab in Oxford (Bluff et al., 2007). To test the notion that tool use was learned by observing older animals, two of the young crows had a keeper who demonstrated tool use in a controlled way, extracting food from crevices with sticks while the little crows watched. The other two were not allowed to see people or other crows using tools. Nevertheless, all four animals began to pick up sticks and poke them into holes at about the same age, and all were soon using them to obtain food. Thus, what is apparently special about the crows—and woodpecker finches as well (see Bluff et al., 2007)—is not their possession of some special tool-related cognitive ability but the tendency to perform early precursors to tool use. These get trial-and-error learning started, although interactions with tool-using adults also play a role (Bluff, Troscianko, Weir, Kacelnik, & Rutz, 2010; Holzhaider et al., 2010).

This study of how tool use develops makes a final important general point: attempting to classify behavior as *learned* as opposed to *innate* is meaningless. Trial-and-error learning likely perfects the crows' skill, but it operates on appropriate motor patterns which they are predisposed to engage in. By the same token, tool use is not innate either, if

by *innate* we mean performed without any relevant experience. And if we mean by *innate* not modifiable by experience once it is performed, that cannot be correct either. Every moment of an organism's development from the very beginning results from a seamless interplay of the learned and the innate, or genes and environment. Genes determine how the environment influences development and subsequent behavior, and the reverse. Nothing in behavior or cognition is either wholly learned or entirely innate. Even species-specific abilities such as bird's singing a certain kind of song are the product of both the individual's species-typical genes and a species-typical developmental trajectory, including contact with singing adults of its species. Thus, as with *intelligent*, classifying behavior as innate or genetically determined versus learned or environmentally determined is meaningless, if indeed it ever made sense outside of folk psychology (Bateson & Mameli, 2007).

Two major approaches to research in comparative cognition converge in the studies of tool use by New Caledonian crows, the traditional psychological or anthropocentric approach on the one hand and the ecological or biological approach on the other. The one tradition focuses on studying cognitive processes in animals (here those underlying tool use) as they may illuminate or resemble processes in humans, whereas the other addresses cognitive mechanisms underlying ecologically relevant behavior in nature and does so in the context of Tinbergen's questions about evolution, function, proximal causation, and development. In the rest of the book we will often be looking at the psychological building blocks of such synthetic research, for example, the effects of reward or the characteristics of memory, based on studies of a few species in the laboratory. But there will also be further examples of ways in which such findings are enriched, challenged, and extended by integrating information from other areas of behavioral biology. In the early twenty-first century anthropocentrism means thinking about the phylogeny and evolution of human cognitive capacities: which are shared with other species by common descent or convergence and which are unique to humans and why. These questions are the focus of Chapter 5.

How This Book Is Organized

This book takes a "bottom-up" approach to comparative cognition, going from basic domain-general processes shared across vertebrates and many invertebrates and building up to apparently more complex domain-specific processes such as social understanding and language.

Thus, it traces Darwin's argument from the processes most widely shared to those possibly unique to humans. This organization also reflects the development of much comparative cognition research within experimental psychology by starting, in Chapter 2, with the processes that have been studied the longest and hence are best understood: animal perception, memory, habituation or learning about single events, associative learning (classical and instrumental conditioning), discrimination, and category learning. With this foundation we can better appreciate the specialized or modular aspects of the processes for dealing with specific domains of physical and social information. Chapter 3 looks at processes specific to acquiring, storing, and acting on information about the physical world: space, time, number, tools and the consequences of action. In Chapter 4 we look at processes specific to individuals' interactions with one another: social learning, imitation, understanding of others' goals and intentions, and communication. Chapter 5 integrates material from the rest of the book by revisiting Darwin's claim that humans differ mentally from other species only in degree, not in kind. We will see that the recent explosion of comparative research has given reason to question Darwin's claim and provided grounds for proposing some quite specific ways in which human cognition is unique as well as yielding new evidence for sophisticated nonverbal processes that we share with other species.

Suggestions for Further Reading

These are mainly books with further depth and detail on the approaches to animal cognition and behavior introduced in this chapter. The Web sites of the Comparative Cognition Society and the Animal Behavior Society are also recommended for links to news and Web sites of individual scientists, many of which have photo and video illustrations of their research.

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- Vonk, J., & Shackelford, T. (Eds.). (2012). *Oxford Handbook of Comparative Evolutionary Psychology*. New York: Oxford University Press.
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Basic Processes

The simplest behavior consists of reflexes, direct connections between sensory channels and response-generating mechanisms. But most behavior of interest in this book implies some more elaborate internal intervening structure or process. For instance, inputs from multiple sensory channels may be integrated into representations of objects and situations. The effects of sensory events may be retained, as evident in changed behavior toward later occurrences of the same events; that is, animals exhibit memory. And repeated encounters with the same temporal or spatial pattern of events may result in learning their relationship.

The basic processes of perception, memory, and learning characterized by these statements are found in all sorts of animals (Papini, 2008). They can be the building blocks of more complex processes such as learning categories and concepts, finding one's way around in space, and navigating complex social networks. Nowadays, applying Morgan's Canon (Chapter 1) often means trying to distinguish behavior based on such simple phylogenetically general cognitive processes from that based on apparently more complex or specialized ones. Indeed, for some authors, only the latter are meaningfully "cognitive" (see Shettleworth, 2010a). However, this book embraces all mechanisms involved in acquiring, storing, and acting on information from the environment, how they work, what distinguishes them from one another, and which species have them. Thus, we begin with basic mechanisms of perception, memory, and learning, and the job of this chapter is to convey them. Along the way we will encounter some important foundational issues. How can we