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Cognition and the Study of Behavior

Walnut trees shade the streets of Davis, California. They also provide food for the crows that roost near Davis. Crows crack walnuts by dropping them from heights of 5–10 meters or more onto sidewalks, roads, and parking lots. Occasionally they drop walnuts in front of approaching cars, as if using the cars to crush the nuts for them. Do crows intentionally use cars as nutcrackers? Some of the citizens of Davis, as well as some professional biologists (Maple 1974, in Cristol et al. 1997) were convinced that they do, at least until a team of young biologists at UC Davis put this anecdote to the test (Cristol et al. 1997). They reasoned that if crows were using cars as tools, the birds would be more likely to drop nuts onto the road when cars were coming than when the road was empty. Furthermore, if a crow was standing in the road with an uncracked walnut as a car approached, it should leave the nut in the road to be crushed rather than carry it away.

Cristol and his collaborators watched crows feeding on walnuts and recorded how likely the birds were to leave an uncracked walnut in the road when cars were approaching and when the road was empty. They found no support for the notion that crows were using automobiles as nutcrackers (Figure 1.1). In other respects, however, the birds' behavior with walnuts was quite sophisticated (Cristol and Switzer 1999). For example, by dropping nuts from buildings on the Davis campus, Cristol and Switzer verified that English walnuts did not have to be carried so high before breaking as the harder black walnuts and that they broke more easily when dropped onto pavement than onto soil. The crows' behavior reflected these facts (Figure 1.1). A crow dropping a nut also took into account the likelihood that a greedy fellow crow might steal a dropped nut before it could be retrieved: the fewer crows waiting on the ground nearby, the higher they took walnuts before dropping them.

The story of the nutcracking crows encapsulates some key issues in the study of cognition in animals. Foremost is how to translate a hypothesis about essentially unobservable internal processes into hypotheses about behavior in a way that permits different explanations to be distinguished. Here, this meant asking, "What will crows do if they are using cars as tools that they will not do if they are merely dropping nuts onto the road as a car happens by?" A second issue has to do with the kinds of hypotheses people entertain about the processes underlying animal behavior. The people in Davis and elsewhere (Nihei 1995; Caffrey 2001) who saw nutcracking as an expression of clever

crows' ability to reason and plan were engaging in an anthropomorphism that is common even among professional students of animal behavior (see below, Section 1.3.2; Kennedy 1992; Wynne 2007a, 2007b). As we will see, such thinking can be a fertile source of ideas, but research often reveals that simple processes apparently quite unlike explicit reasoning are doing surprisingly complex jobs. Free-living crows were observed doing something suggestive of interesting information processing and decision making. Their behavior was then examined with more systematic observations and experiments. Among other things, these revealed how closely the crows' behavior matched environmental requirements. Numerous cognitive processes underlie the crows' nutcracking, and each of these could be analyzed further. For example, how do crows judge the height from which they drop nuts? Do they have to learn to adjust their behavior to the kind of nut, the kind of substrate, and the number of nearby crows? Several species of crows, gulls, and other birds break hard-shelled prey by dropping them (Cristol and Switzer 1999), and one might also ask what ecological conditions or evolutionary history favor this behavior.
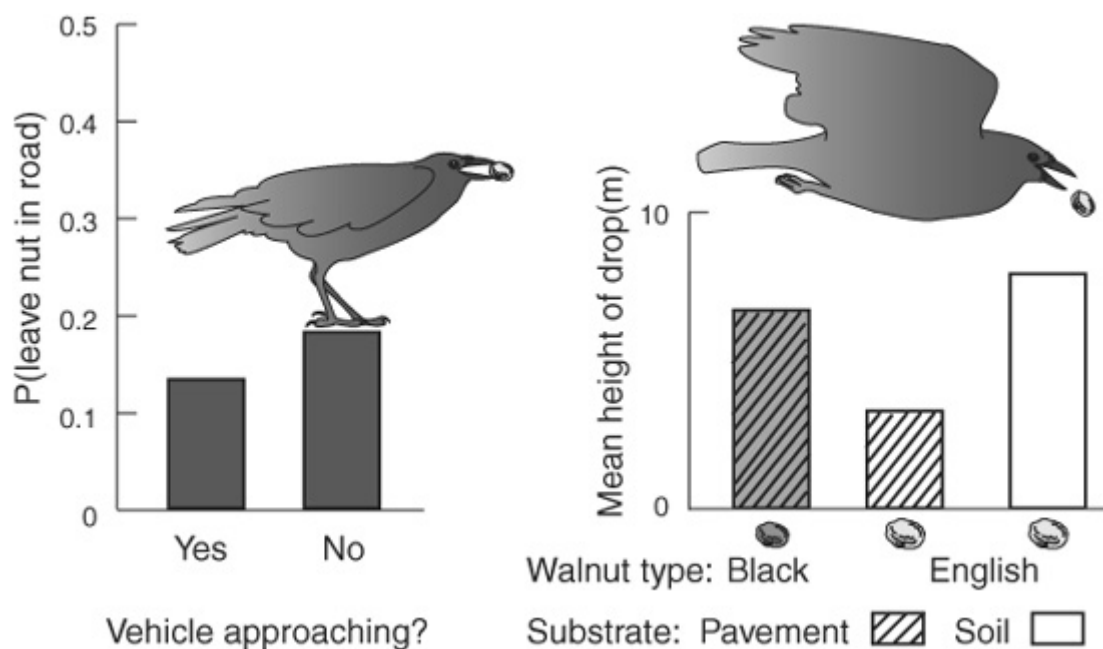

Figure 1.1. Left: Proportion of crows dropping a walnut in the road when flying away as a function of whether or not a vehicle was approaching (data from Cristol et al. 1997). Right: Mean height to which crows carried black or English walnuts before dropping them onto pavement (cross-hatched bars) or onto soil (English walnuts only) (data from Cristol and Switzer 1999).

1.1 What is comparative cognition about?

1.1.1 What is cognition?

Cognition refers to the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making. The study of comparative cognition is therefore concerned with how animals process information, starting with how information is acquired by the senses. The behavior examined for evidence of cognition need not be learned, and it need not be studied in the laboratory by psychologists. In this book how birds classify songs in the field will be considered alongside how animals can be taught to classify artificial stimuli in the laboratory (Chapter 6). Possible natural examples of tool use like the crows' nutcracking will be examined along with tests of what captive animals understand when they use tools (Chapter 11). The dance communication of bees and the alarm calling of chickens will be considered alongside the use of human gestures, words, and symbols by parrots and chimpanzees (Chapter 14). How ants find their way in the desert and how rats find their way in mazes will both be examined for what they reveal about the principles of spatial cognition (Chapter 8).

Not all agree that such an inclusive definition of cognition is useful. *Cognitive* is often reserved for the manipulation of declarative rather than procedural knowledge (e.g., Dickinson 2008). Declarative knowledge is "knowing that" whereas procedural knowledge is "knowing how," or knowing what to do. The declarative knowledge that a chipmunk might gain from moving about its territory could be maplike: "Home burrow is south of that big rock." Or the chipmunk might store information about its territory as procedural knowledge such as "Turn left at the rock." The first kind of representation implies more flexible behavior than the second, but in both cases behavior results from processing and storing information about the world. A related distinction is that between first-order and higher-order processes, only the latter of which may be regarded as interestingly cognitive. First-order processes operate directly on perceptual input, as when a stimulus triggers a response or creates a trace in memory. Second-order processes operate on first-order processes, as in evaluating the strength of one's memory for an event (Heyes 2008; Penn, Holyoak, and Povinelli 2008).

For many psychologists, mental representations of the world or computations on them are the essence of cognition. However, it is almost never possible to tell without experimental analysis what kinds of processes are reflected in a given behavior. Moreover, functionally similar behavior, such as communicating, recognizing neighbors, or way finding, may be accomplished in different ways by different kinds of animals (Dyer 1994). Much interesting adaptive behavior results from processing limited information in simple ways, and the richness of the representations underlying behavior varies considerably across species and behavior systems. Because comparing the ways in which

different species solve similar information-processing problems is an important part of the comparative study of cognition, it should embrace all sorts of information processing and decision-making.

1.1.2 *Animal* cognition or *comparative* cognition?

Referring to the field of research discussed in this book as *comparative* rather than *animal* cognition is similarly inclusive. Some classic assessments of psychological research on animals (Beach 1950; Hodos and Campbell 1969; Dewsbury 1998) are complaints that most studies labeled "comparative" are mere "animal psychology" because they deal with only a single nonhuman species or at most implicitly compare that one species with humans. As we will see, the situation in the early twenty-first century is dramatically different. More species are being studied and compared with one another, and findings are interpreted with increasing biological sophistication. But there is still a good deal of research aimed at analyzing particular processes in depth in one or a few species. It is especially prominent in the section of this book on Basic Processes (Chapters 3–7). But thorough analyses of cognitive processes in limited species form the foundation for comparative work, as when comparisons of memory in food storing and nonstoring birds (Chapters 2 and 7) draw on method and theory developed in studies with pigeons. Therefore "animal cognition" research is part of the overarching enterprise referred to in this book as research on comparative cognition aimed at understanding cognition across the animal kingdom, including how it works, what it is good for in nature, and how it evolved.

1.1.3 Consciousness and animal cognition

People intuitively distinguish between merely responding to events and being aware of them, as when someone driving along a busy highway while deep in conversation says, "I wasn't conscious of the passing miles." Perceptual awareness can be distinguished from reflective consciousness, which might be evidenced when the driver mentally compares possible routes to her destination, perhaps evaluating her own ability to recall their details (self-reflective consciousness).

Within psychology, the rise of behaviorism in the early 1900s threw introspective studies of consciousness into disrepute. The cognitive revolution of the 1960s and 1970s continued this tradition. Studying cognition meant inferring how information is processed from analyzing input-output relations without regard for the extent or kind of concomitant awareness. But in the last decade or so of the twentieth century, the study of consciousness in humans and other species became not only scientifically respectable but an active area of research. One impetus for this work

was the discovery of striking phenomena such as "blindsight" (Box 1.1) and priming in memory (Chapter 7), which reveal distinct conscious and unconscious processes in everyday cognition. Debates about the extent to which people are aware of their own cognition (metacognition; Chapter 7) have also placed a new emphasis on how subjects consciously experience their memories, percepts, or the like as distinct from how they act on them. Progress in analyzing the neural basis of behavior in such experiments through brain imaging and studies of cognitively impaired people have encouraged attempts to investigate the same processes in animals (e.g., Terrace & Metcalfe 2005). If some pattern of brain activity turns out to be necessary and sufficient for verbal reports of conscious awareness, thinking, remembering, or the like, what does it mean if this same pattern can be identified in an animal?

Box 1.1 Vision with and without Awareness

Neurological patients with "blindsight" react to objects in the visual field without reporting awareness of them (Weiskrantz 1986). If such patients, who have damage in area V1 of the visual cortex, are shown an object in the affected part of the visual field, they report seeing nothing. However, when they are forced to point to the object's location or guess its characteristics, they perform above chance. Thus these people seem to have vision without awareness. Visual detection apparently can be dissociated from visual awareness in monkeys, too (Cowey and Stoerig 1995, 1997). Three monkeys with lesions to area V1 were trained in two different tasks (Figure B1.1). One was analogous to asking them "Do you see it?" and the other, to asking them "Where is it?" The lesions affected only the right half of each monkey's visual field, so each monkey's performance to stimuli there could be compared to its performance when stimuli were shown in the field with normal vision. To control the part of the retina stimulated, displays were presented briefly while the monkey was fixating a spot in the middle of a computer screen.
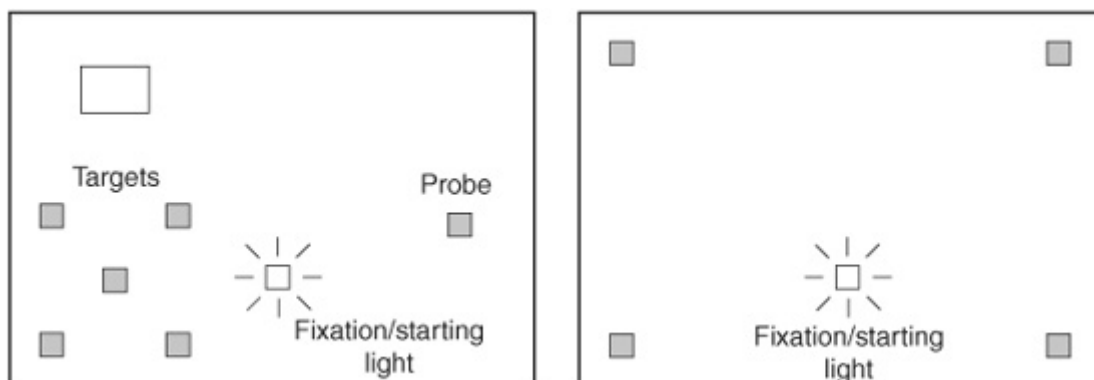
Figure B1.1. Stimulus displays for testing blindsight in monkeys. Redrawn from Cowey and Stoerig (1995) with permission.

To train the monkeys to report "I see it," a stimulus was presented any of five positions in the lower part of the normal field, and on some trials no stimulus was presented (Figure B1.1, left). In the former case, the monkey was rewarded for touching the location where the stimulus had appeared. In the latter, it was rewarded for reporting "no" by touching a white rectangle at the top of the screen. When the monkeys were reporting presence/absence correctly on about 95% of the trials, they were tested with occasional probes in the "blind" half of the visual field. They reported "no stimulus" about 95% of the time. Importantly, a normal control monkey did transfer correct responding to this novel location. In the other task, a brief flash appeared in one of the four corners of the screen on every trial (Figure B1.1, right). The monkeys had simply to touch the location where it had appeared, in effect reporting where they saw it. In this task, performance was highly accurate for both the normal and the "blind" visual field. These data are consistent with other evidence that primates have separate visual pathways for perception and action (Goodale and Milner 1992). Like people with comparable brain damage, the monkeys appear to have vision without awareness in the affected part of the visual field, suggesting that their normal vision is accompanied by awareness.

In this example, nonverbal responses that the monkeys were trained to make substituted directly for humans' verbal reports ("I see it," etc.). When people with blindsight took the same nonverbal tests as the monkeys, their responses paralleled their verbal reports of awareness (Stoerig, Zontanou and Cowey 2002).

A central methodological problem here is that because evidence for consciousness in humans generally consists of what people say about their mental experiences, seeking it in nonverbal species requires us to accept some piece of the animal's behavior as equivalent to a person's verbal report. For example, in the experiment described in Box 1.1, we must accept that the monkeys' "I see it" response indexes a subjective state equivalent to a person's experience of seeing. Clearly we can never know whether this is correct or not, since we can never know the animal's private state. Therefore, the point of view of most researchers studying animal cognition is that how animals process information can, and should, be analyzed without making any assumptions about what their private experiences are like. That is, the best we can do is to seek *functional similarities* between behaviors taken as evidence for given processes in humans and behaviors of animals (Staddon 2000;

Hampton 2005; Heyes 2008). This approach takes support from evidence that people act without being aware of the reasons for their actions, that is, without using reflective consciousness, more often than is commonly realized. We may, for example reach for the reddest tomato on the bush and only later explain why (Carruthers 2005). A related view (Macphail 1998) is that human babies nor nonhuman animals can have reflective consciousness because it requires language.

The view that consciousness in animals is not a subject for research either because it is inaccessible to scientific study or because animals lack language was emphatically rejected by scientists calling themselves cognitive ethologists (Ristau 1991a). Stimulated by the writings of the distinguished biologist Donald Griffin (1976, 2001), cognitive ethologists claim that much behavior suggests that animals have conscious intentions, beliefs, and self-awareness, and that they consciously think about alternative courses of action and make plans (Griffin and Speck 2004). Studies of animals communicating, using tools, and apparently deceiving one another figure prominently in these discussions because they seem to reveal flexible behaviors governed by intentions to achieve specific goals. However, it is difficult to find a situation for which the notion that an animal has a conscious belief or intention or is consciously manipulating information unambiguously predicts what it does (Dawkins 1993; but see Griffin 2001). Nevertheless, the early years of the twenty-first century have seen an upsurge of provocative and sometimes controversial research addressed to exactly these issues.

Of course, some anthropomorphic mentalistic terms have traditionally been accepted to refer to processes underlying animal behavior. For example, training a rat that a tone predicts a shock is usually referred to as fear conditioning. The rat is said to fear the tone, and indeed it may be in the same physiological state as a person describing himself as fearful. Similarly, a hungry rat trained to press a lever for food could be said to be doing so because it desires food and believes that lever pressing will give it food. On one view (Chapter 11 and Dickinson 2008) the goal-directedness of bar pressing or other instrumental responding, that is, evidence that it is controlled by belief and desire, is what is meant by its being under cognitive control. Belief, desire, fear, or other mental or emotional states may be ascribed to animals on the basis of well-defined behavioral criteria, that is, on the basis of functional similarity, without implying that the animals are undergoing humanlike conscious experiences.

Thinking about how consciousness might have evolved is not much help here. On the one hand, if we accept that human beings are conscious it seems that some other species, perhaps among primates, must share at least perceptual awareness with humans (see Terrace and Metcalfe 2005). Saying that only humans are conscious in any way seems like rejecting evolutionary continuity (but

see Penn, Holyoak, and Povinelli 2008). On the other hand, because evolution has acted via the results of what creatures do, not directly on what they experience privately while doing it, it seems there must be something promoting survival and reproduction that a conscious animal can do and one lacking consciousness cannot, but so far there are no clear candidates for that "something" (Dawkins 1993, 2006). This same problem of an apparent evolutionary gap between humans and other living species arises in discussions of the evolution of human language and abstract conceptual abilities (Chapter 15 and Penn, Holyoak, and Povinelli 2008). Despite the apparent successes of teaching aspects of language to apes, most would now conclude that language is unique to humans, and the conditions under which it could evolve are an active area of debate (Chapter 14). Anthropological studies of human evolution and of primate behavior in the wild are likely to add fuel to these discussions for some time to come.

1.1.4 A word about *intelligence*

It is sometimes said by cognitive ethologists (Griffin 1992) and popular writers (e.g., Barber 1994) that animals must be thinking because they behave so intelligently. Indeed, to the nonspecialist one of the most persuasive arguments that animals think as we do is that it is impossible to imagine another explanation for their "clever" behavior (Blumberg and Wasserman 1995; Wynne 2004a). On the whole, however, *intelligence* is not a useful term for describing animal behavior, for two reasons. First, intelligence is generally used to describe global ability in people, whereas the cognitive abilities of animals (and perhaps people as well) are to a large extent modular (Box 2.3). For instance, a Clark's nutcracker that can retrieve thousands of pine seeds months after caching them (Box 1.4) is not necessarily "smart" in other ways. It is particularly good at encoding and retaining certain kinds of spatial information, but it may remember other kinds of information no better than other birds. Within this context, *intelligence* is sometimes used nowadays to refer to the collection of specific cognitive abilities that a species may have (cf., Emery 2006; Pearce 2008).

A second reason to use *intelligence* carefully is that it should be defined formally with respect to a specified goal (McFarland and Bosser 1993). A robot is intelligent with respect to a goal of efficiency if it minimizes use of its battery while when crossing a room. It is intelligent with respect to the goal of remaining intact if it avoids collisions. On this view, biological intelligence should be defined in terms of fitness (Box 1.2 and Kacelnik 2006) or goals such as choosing a good mate that contribute to fitness, and even plants can be intelligent (Trewavas 2002). Sometimes, as we will often see in this book, intelligent behavior may be produced by very "unintelligent" means.

Box 1.2 Natural Selection and Fitness

Evolution, the change in the characteristics of organisms over generations, occasioned much debate before Charles Darwin (1859) and Alfred Russel Wallace explained how it happens. Fossils indicated that very different kinds of animals and plants had existed in the past. Explorers, including Darwin and Wallace themselves, documented how animals and plants in different parts of the world are both similar and different. What Darwin and Wallace did, independently at about the same time, was to show how both the changes in organisms over time and the relationships among them can be explained by a natural cause. That cause is *natural selection*, and it is the inevitable outcome of three fundamental properties of all living things.

1. Offspring inherit their parents' characteristics. Bean seeds produce more bean plants, robin eggs produce more robins, and many of their features will be more like those of their parents than others of the same species. We now know a great deal about the genetic mechanisms involved, but the principle of *inheritance* is independent of such knowledge, which Darwin and Wallace did not have.

2. There is *variation* among individuals within the same species, even when they are closely related.

3. *Selection* takes place. A sea turtle lays hundreds of eggs, an oak tree drops hundreds of acorns, yet the world is not overrun with sea turtles or oak trees. Only those best able to survive in the current environment will live to reproduce. This principle is sometimes summarized as "the survival of the fittest." In technical terms, *fitness* refers to an organism's ability to leave copies of its genes in the next generation, not to what people get at the gym. A male who sires ten healthy offspring is fitter than one who sires two. Because relatives share some of one's own genes, fitness can be enhanced through helping them as well as direct offspring (Chapter 5).

Evolution is the inevitable consequence of inheritance, variation, and selection. Gradually, over many generations, individuals with characteristics that made their ancestors best able to survive and reproduce will come to predominate. Individuals that migrate or are carried into new environments may evolve such different characteristics that eventually their descendents will form a new species, unable to breed with individuals of the ancestral species (see Grant and Grant 2008). Throughout the last part of the twentieth century evolutionary theorists, including most of

the founders of behavioral ecology, emphasized selection at the level of the individual, indeed the individual's genes. On this view, the genes best able to program the organisms bearing them to develop into individuals that propagate successfully will be the ones that persist over generations (R. Dawkins 1976, 1995). However, the logic of inheritance, variation, and selection applies to units at all levels, most importantly for contemporary theorizing, even to groups of individuals. After being emphatically rejected for nearly 40 years, evolution through selection at the level of groups is now becoming accepted as part of a broad theory of multilevel selection (Wilson and Wilson 2007, 2008). Group and individual selection may pull in different ways, but the characters that benefit the group at the apparent expense of the individual may still be advantageous over the long run. Among other things, the force of group selection helps to explain some of the unique features of human psychology such as a tendency to cooperate and empathize with unrelated others (Chapter 12 and Wilson and Wilson 2007, 2008).

Finally, labeling behavior *intelligent* is pretty frankly both anthropomorphic and anthropocentric. Recent demonstrations that species differ in behavioral flexibility, or propensity to adopt novel foraging behaviors (Box 2.2), have revived discussions of overall animal intelligence (cf., Roth & Dicke 2005). This is especially so because the correlation of flexibility with overall brain size and/or size of the forebrain in some animal groups (Box 2.2) satisfies the everyday equation of intelligence with "braininess." The naively anthropocentric nature of such discussions is underlined by a comparison of pigeons and people in a test of complex reaction time (Vickrey and Neuringer 2000). In such a test the subject is confronted with an array of lights; a randomly chosen one, the target, lights up on each trial and the subject's task is to touch it as quickly as possible. Human subjects take longer to respond as the number of lights in the array increases, but people with high IQ show the smallest increase. It is claimed this is because high IQ reflects a general ability to process information fast. On this analysis, "less intelligent" species should be affected more strongly by increasing numbers of targets than humans. In fact, however, pigeons show a smaller effect than very intelligent humans (students at the highly selective U.S. Reed College) tested in the same way, maintaining a fast response speed as target number increases. As the authors of this study observe, "the counterintuitive conclusion follows that pigeons are more intelligent than people. An alternative view assumes that different *intelligences* or factors are employed in different situations by different individuals, groups, and species" (Vickrey & Neuringer, 2000, 291).

1.2 Kinds of explanation for behavior

1.2.1 Tinbergen's four questions

The pioneering ethologist Niko Tinbergen (1963) emphasized that the question, "Why does the animal do that?" can mean four different things, sometimes referred to as "Tinbergen's four whys." "Why?" can mean "How does it work?" in the sense of "What events inside and outside the animal cause it to behave as it does at this moment?" This is the question of the proximate cause (or simply cause) of behavior. Perceptions, representations, decisions, as well as the neural events that accompany them, are all possible proximate causes of behavior (Hogan 2005). One might also ask about development in the individual, that is "How do experience and genetic makeup combine to cause the animal to behave as it does?" "Why" can also mean "What is the behavior good for; what is its survival value?" This is the question of function or adaptive value. Finally, one can ask how a particular behavior evolved, as inferred from the phylogeny of species that show it (Chapter 2) together with evidence about its current function (Cuthill 2005). Causation, development, function, and evolution are not levels of explanation but complementary accounts that can be given of any behavior. As Tinbergen emphasized, a complete understanding of behavior includes answers to all four questions. However, it is important to be clear on how they differ from one another and to avoid confusing the answer to one with the answer to another.

Consider as an example some possible answers to the question raised at the beginning of this chapter, "Why do crows drop walnuts?" The proximate cause of nut dropping would be sought in some interaction of the bird's internal state, most likely hunger, with external stimuli like the presence of walnuts, other crows, and hard surfaces. Proximate causes can be specified at levels right down to events at the level of genes and neurons, but often causal mechanisms are inferred from input-output relations at the level of the whole animal (Hogan 2005). This is generally true with the sorts of cognitive mechanisms discussed in this book. Explanations of the immediate causes of behavior do not include teleology, or reference to conscious purposes or goals (see Hogan 1994a). The future cannot cause what is happening in the present. The crow does not drop walnuts "to get food" though it is possible that she does so because similar behavior in the past was followed by a tasty snack, that is, because of past reinforcement. Examining the bird's history of reinforcement would be part of a developmental explanation, as would an account of any other factors within the crow's lifetime that affected its nut dropping.

The immediate function, or adaptive value, of behavior is what it is good for in the life of the individual. Cracking walnuts clearly functions in obtaining food, but questions about the function of

the crow's behavior can also asked at finer levels of detail. For instance, the functional question, "Why carry a nut so high and no higher?" was tackled by testing whether the height to which nuts are carried matched the type of nut and where it was dropped (Figure 1.1, see also Zach 1979).

Tinbergen's fourth question, "How did it evolve?" usually has to be tackled by trying to look at the behavior's phylogenetic history using methods described in Chapter 2. For the crows' nutcracking, this would include discovering whether close relatives of American crows also drop hard-shelled prey items and whether specific ecological conditions are associated with prey-dropping (Cristol and Switzer 1999). Occasionally it has been possible to observe evolution happening in the wild as natural populations have changed rapidly in response to changes in selection pressures (e.g., Endler 1986). Some of these examples involve behavior at least implicitly. For instance, in a famous long-term field study, Rosemary Grant and Peter Grant observed the beaks of seed-eating finches on the Galapagos Islands changing in response to drastic changes in rainfall (Grant and Grant 2008). In years of drought, only the birds most skilled at cracking the few remaining seeds could survive and reproduce. Beak depth, an indication of seed-cracking power, contributed importantly to survival in the medium ground finch (*Geospiza fortis*). Because beak depth is heritable, changes in the population's distribution of beak depths could be detected in a few generations (Figure 1.2). The birds' behavior must have changed, too, perhaps through learning. Rather than ignoring the hardest seeds, as they did in times of plenty, the successful individuals evidently became skilled at finding and cracking them.

In terms of Tinbergen's four questions, cognition is one of the proximate causes of behavior. Because studying cognition may include analyzing how information and ways of responding to it are acquired, studying cognition may also involve studying development. Throughout this book we will be concerned with the adaptive value and evolution of cognitive mechanisms. But speaking of cognition doesn't imply that animals are aware of the effects that their actions have on fitness. Evolution produces machines that reproduce themselves (Box 1.2). A robin builds a nest and lays eggs. It responds to eggs by incubating them. As a result of the parents' keeping the eggs at a temperature they have evolved to develop at, young robins hatch with nervous systems so constructed that they open their beaks and beg when an adult approaches the nest. The adult's nervous system responds to gaping by inserting food, and so on. The bird isn't responding to "my young," let alone planning to have lots of grandchildren, but to stimuli that are generally reliable correlates of offspring like gaping mouths in its nest. Behavioral mechanisms, including cognitive processes such as memory for the location of the nest and tuning of the adults' perception to the signals emitted by the young, are selected if they increase their bearer's representation in future

generations, but such mechanisms need not—and seldom, if ever, do—include foresight into the effects of behavior on fitness (Chapter 11).
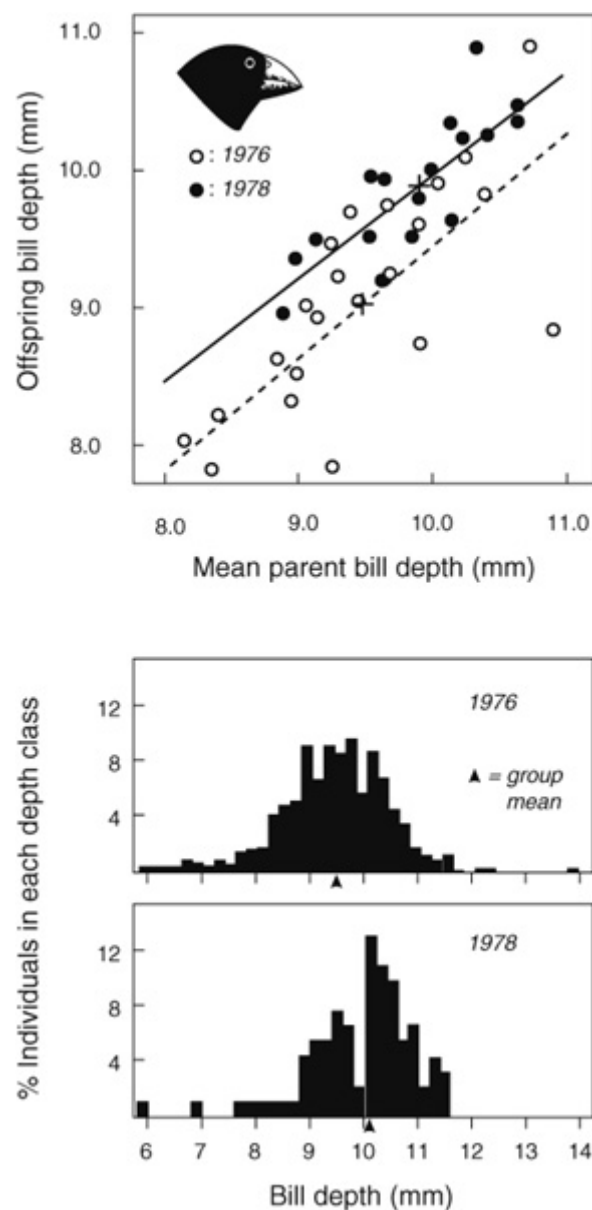

Figure 1.2. Upper panel: Inheritance of bill depth (height of the bill in the drawing) in medium ground finches in two different years. Slope of the line relating offspring to parent bill depth—a measure of heritability—was almost the same in both years. Variation and selection of bill depth are illustrated in the two lower panels. In 1978 there was a drought, and the finches could subsist only by cracking the hardest seeds, accounting for the greater survival of those with deeper bills. Redrawn from Boag and Grant (1984) and Boag (1983) with permission.

1.2.2 "Learned" and "innate" behavior

Learning is often contrasted with genetic or innate control of behavior. What this dichotomy overlooks is that learning is possible only for an animal whose genes and prior environment have resulted in development of an individual ready to be affected by experience in a certain way. No behavior is either strictly learned or entirely innate. An excellent illustration of how preexisting selective processes in the animal interact with specific experiences to produce learning comes from classic comparisons of song learning in two species of sparrows (Marler and Peters 1989). Like many other songbirds (Box 13.2), male song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*) need to hear species-specific song early in life in order to sing it when they mature. The two species are closely related, but swamp sparrows sing a much simpler song.

Marler and Peters played song sparrow songs and swamp sparrow songs to isolated young males of both species in the laboratory. Thus, all the birds had the same acoustic experience. But their behavior as adults revealed that they had learned different, species-appropriate things from it (Figure 1.3). Swamp sparrows learned only swamp sparrow songs, and song sparrows had a strong preference to learn song sparrow songs. The interaction of species with experience is still seen even when the birds are raised in the laboratory from the egg or very early nestling stage, showing that it probably does not result from birds hearing their father's song. Because birds of each species sometimes do produce sounds characteristic of the other species, it seems unlikely that the species difference in song production results from a motor constraint. In the wild, these two species may live within earshot of each other, so early-developing selectivity in perception and/or learning likely functions to ensure that each one learns only its own species song. Indeed, young birds still in the nest respond most to their own species song, as shown by the way heart rate changes when they are played different sounds (Marler and Peters 1989).

This example comes from a specialized behavior shown by only a few of the world's species, but it makes a very important general point: cognitive mechanisms are adaptations to process and use certain kinds of information in certain ways, not mechanisms for information processing in general. As for the theme of this section, insofar as it implies that genes can work without an environment to work in, the term *innate* is never appropriate in modern biology (Bateson and Mameli 2007). However, we do sometimes need a term for the many behaviors that appear in development ready to serve their apparent function before they can have done so. For instance, selecting the species-typical song for learning clearly serves the function of allowing the adult male, many months later, to sing in a way that his conspecifics are most responsive to. Hogan (1994b) has suggested the term *pre-*

functional for such cases, because it does not imply that the genes have worked in isolation nor that prior experience is irrelevant. However, because this term implies that we know the function of the behavior, *predisposition* or *preexisting bias* may be preferable.

Finally, to say that some behavior or cognitive process develops prefunctionally is not to say that it is unmodifiable (Dawkins 1995). As the comparison of song and swamp sparrows illustrates, how much and in what ways behavior can be modified itself reflects events earlier in development. This example also shows how a stereotyped behavior seen in most normally developing members of a species can result from learning. However, although it makes a key point for this book in showing how experience can have species-species effects, it misleadingly implies that effects of experience (here, the songs) and genes (the species of sparrow) can always be neatly separated. Developmental biologists are increasingly documenting gene by environment interactions and interdependencies as well as epigenetic effects, in which environmental effects on the genes of one generation are passed on to the next (Sokolowski & Levine in press). Some of these discoveries have implications for behavior; undoubtedly more such will be uncovered in the future.
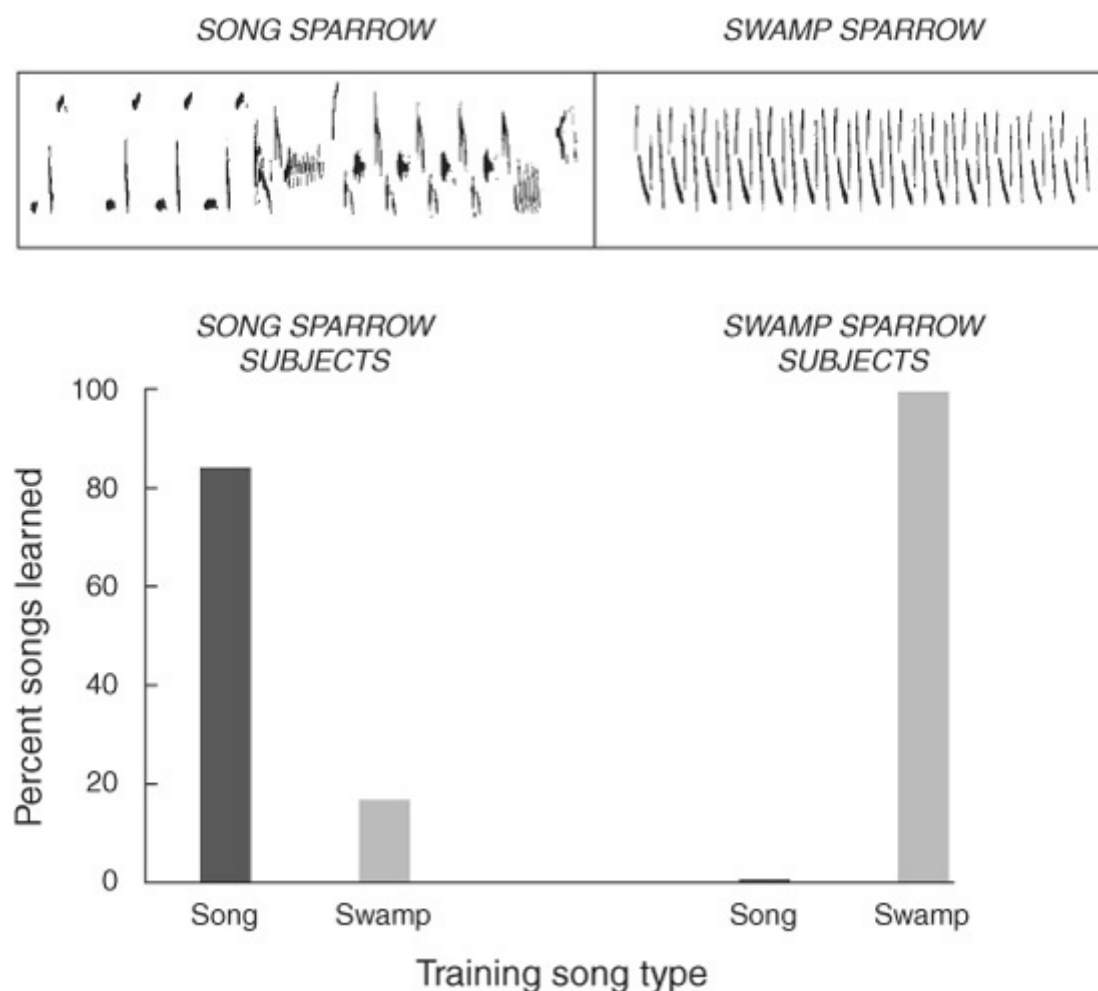
Figure 1.3. Song sparrows and swamp sparrows exposed to both song sparrow and swamp sparrow songs when young learn primarily the songs of their own species. Top panel shows sonagrams (sound frequency vs. time) of songs from normal adults of the two species. Redrawn from Marler and Peters (1989) with permission.

In conclusion, structure as well as behavior, the animal's *phenotype,* results from a continuous and seamless interplay of genes and environment that is itself selected. The extent to which behavior patterns or cognitive capacities are modifiable by experience varies so much as to make the terms *learned* and *innate* (or *nature* and *nurture*) obsolete (Bateson and Mameli 2007). The fact that individuals within a species (i.e., with a common *genotype*) may develop different physical and/or behavioral phenotypes in different environments is known as *phenotypic plasticity*. The ability of individuals to learn details of their own environment that are unpredictable on an evolutionary timescale is but one aspect of the more general phenomenon of adaptive phenotypic plasticity (Dukas 1998; for a brief review see Agrawal 2001; for further discussion of the topics in this section see Marler 2004).

1.3 Approaches to comparative cognition

Psychologists and biologists have traditionally taken different approaches to studying learning and cognition in animals. These two contrasting traditions have been called, among other things, the study of general processes and the study of adaptive specializations (Riley and Langley 1993) or the General Social Science Model and evolutionary psychology (Cosmides and Tooby 1992). Psychologists have tended to ask, "Can animals do what people do, and if so how do they do it?" whereas biologists tend to ask, "Why, in all Tinbergen's four senses, do animals do what they do in the wild?" Thus the contrast between traditional psychological and biological approaches is one between anthropocentric, or human-centered, and ecological, animal-centered, approaches. It is also one between a field centered on mechanism, just one of Tinbergen's four questions, and one in which "Nothing makes sense except in the light of evolution" (see e.g., Plotkin 2004)

1.3.1 The anthropocentric approach

Comparative psychology began with Darwin's claim—profoundly shocking at the time—that humans are similar to other species in mental as well as physical characteristics. Chapter 3 of his second book, *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), touches on almost every problem that has been studied by comparative psychologists since. In it, Darwin claimed that

other animals differ cognitively from humans in degree but not in kind. That is to say, animals share human abilities such as reasoning, memory, language, and aesthetic sensibility, but generally they possess them to a lesser degree (see Chapter 15). His emphasis was on continuity among species rather than diversity, the other side of the evolutionary coin (Rozin and Schull 1988). Acceptance of continuity has led to using animals in psychology as little furry or feathery people, model systems for studying general processes of learning, memory, decision-making, even psychopathology and their neural and genetic underpinnings. Thus this approach can be characterized as *anthropocentric* because it is concerned primarily with issues related to human psychology.

Around the beginning of the 1900s psychologists' study of cognitive processes in animals began to focus on associative learning (see Boakes 1984). Some researchers in the first part of the twentieth century did study issues such as animal reasoning or insight learning (Dewsbury 2000), but animal cognition as a recognized subfield did not take off until the 1970s (Hulse 2006). Its practitioners were concerned to distinguish themselves from S-R psychologists, who explained behavior in terms of connections between stimuli and responses established by classical or instrumental conditioning and eschewed speculation about unobservable processing of information. Psychologists studying animal cognition, in contrast, used behavior as a window onto processes of memory and representation (Wasserman 1984). Initially, much of their research used learned behavior of rats and pigeons in the laboratory to analyze processes that were being successfully studied in people, such as memory for lists of items, concept formation, and attention (cf., Hulse, Fowler, and Honig 1978).

Research on animal cognition based on the anthropocentric approach has three important characteristics. First, it focuses on memory, representation, and other kinds of information processing that can be identified in people. Second, such research is implicitly comparative, in that other species like parrots or pigeons are compared with humans, but the choice of species is often based more on convenience than on evolutionary considerations. Finally, traditional discussions of anthropocentric research were pervaded by the incorrect and misleading notion of a phylogenetic scale or *scala naturae* (Hodos and Campbell 1969). This is the idea that evolution is a continuous ladder of improvement, from "lowly" worms and slugs, through fish, amphibians and reptiles, to birds and mammals. Humans, needless to say, are at the pinnacle of evolution in this scheme. But present-day species cannot be lined up in this way (Chapter 2). People are not more highly evolved fish, birds, rats, or even chimpanzees. Correct inferences about the relationship between cognitive or brain processes in humans and those in nonhumans depend on a detailed appreciation of the biology of "animal models" (Preuss 1995 ; Papini 2008). Nevertheless, studying a few very diverse species, as in the research sketched in Box 1.3, may be the best way to reveal processes general to all species

(Bitterman 2000; Papini 2002). Exactly this approach to genome mapping has provided stunning support for generality: species as diverse as fruitflies, mice and humans are turning out to share unexpected numbers of genes and basic developmental processes (see Robinson 2004; Papini 2008). In addition, the rigorous methodology and the principles developed with traditional psychological studies of animals are essential to more biologically focused research (e.g., Timberlake, Schaal, and Steinmetz 2005).

Box 1.3 Traditional Comparative Psychology: An Example

In the 1960s and 1970s, M. E. Bitterman and his associates carried out an extensive program of research comparing the performance of goldfish, painted turtles, pigeons, rats, and monkeys on a number of standard laboratory tasks (Bitterman 1965, 1975). Later, this work was extended to honeybees (see Bitterman 2000). Their overall aim was to test the assumption that the "intelligence" of "lower" animals differed only in degree and not in kind from that of "higher" animals. Of course, as Bitterman (1975, 2000) recognized, these species are not on an evolutionary ladder but at the ends of separate branches of the tree of life (Figure B1.3). Therefore, commonalities must reflect either their presence in some very ancient common ancestor or convergence due to similar environmental pressures Bitterman devised ingenious versions of standard apparatuses to present the same kinds of tasks to these very different species. Fish pushed paddles for a reward of worms; pigeons pecked lighted disks for a few grains of corn; turtles crawled down small runways. In one series of experiments, the animals were compared on their ability to learn *successive reversals* of simple visual and spatial discriminations. In successive reversal (Chapter 6) an animal is first rewarded for choosing a certain one of two simultaneously presented stimuli, say red rather than green. After a number of trials, the rewarded stimulus is reversed, for example, the animal must choose green rather than red, and so on. "Intelligent" behavior is to improve over successive reversals, eventually performing perfectly after just one trial on each new problem. Within each species, performance on visual discriminations (e.g., red vs. green for species with color vision or black vs. white for those without) was also compared to performance on spatial (e.g., left vs. right) discriminations. Monkeys, rats, and pigeons improved on both visual and spatial reversals, fish improved on neither, and turtles improved on spatial but not visual reversals. What results from this kind of selection of species and problems can reveal about "the evolution of intelligence" is discussed further in Chapter 2 (see also Papini 2002, 2008).
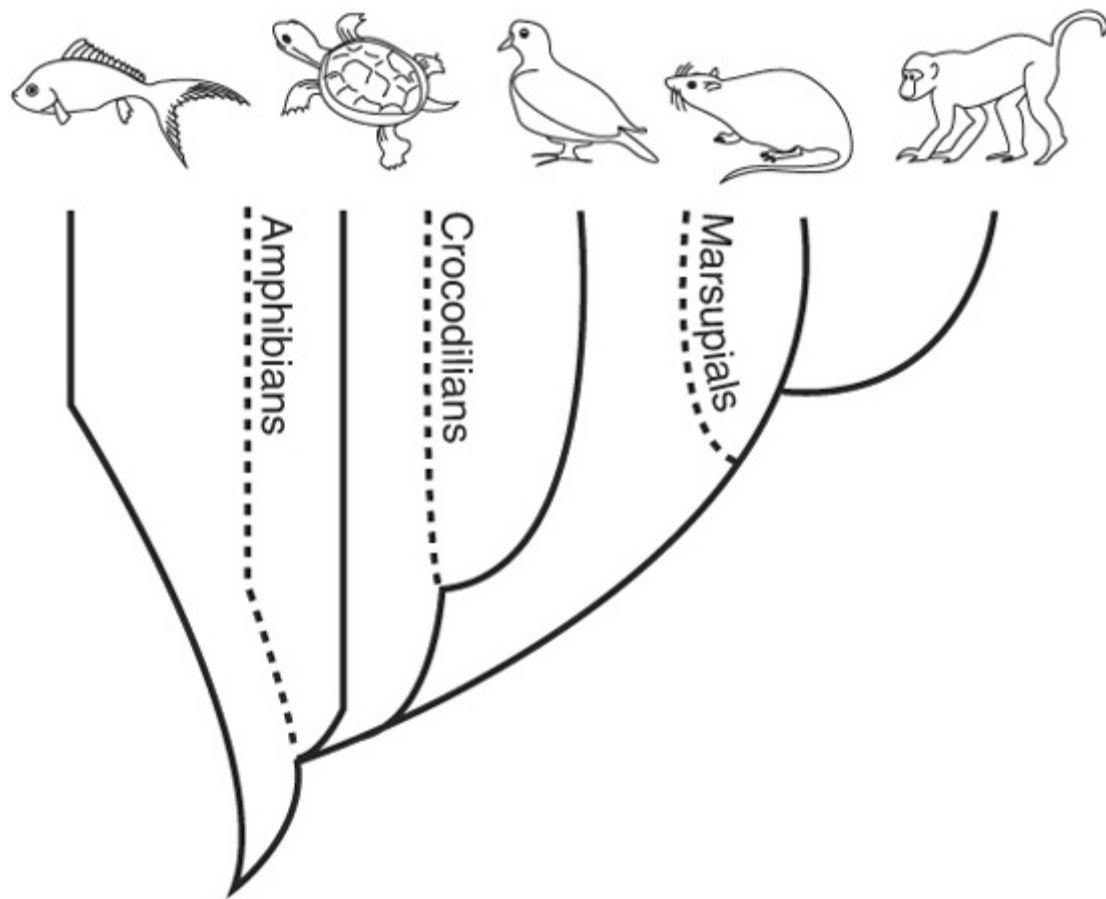
Figure B1.3. A simple phylogeny (see Chapter 2) of the species tested by Bitterman and his colleagues in comparative studies of learning. Neither the recency with which one group is thought to have diverged from another nor its left-right arrangement in such a diagram necessarily implies anything about "intelligence." Redrawn from Bitterman (1975) with permission.

1.3.2 Anthropocentrism, anthropomorphism, and Morgan's Canon

Documenting human-like "mental powers" of animals was central to the agenda of early defenders of Darwinism. Similarity between human and animal minds would surely be the most convincing evidence of evolutionary continuity between humans and other species. Accordingly, some of Darwin's supporters, primary among them George Romanes (1892) set out to collect anecdotes appearing to prove animals could think and solve problems the way people do. Their approach was not just anthropocentric but frankly *anthropomorphic*, explaining animals' apparently clever problem solving in terms of human-like thinking and reasoning. But as we have seen in the case of the nutcracking crows, just because an animal's behavior looks to the casual observer like what a person

would do in a similar-appearing situation does not mean it can be explained in the same way. Such reasoning based on analogy between humans and other animals must be tested with experiments that take into account alternative hypotheses (Heyes 2008).

Fortunately for progress in understanding animal cognition, critics of extreme anthropomorphism were not slow to appear. E. L. Thorndike's (1911/1970) pioneering experiments on how animals solve simple physical problems showed that gradual learning by trial and error was more common than human-like insight and planning (Galef 1998). C. Lloyd Morgan also observed animals in a systematic way but is now best known for stating a principle commonly taken as forbidding unsupported anthropomorphism. What Morgan (1894) called his Canon states, "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." Morgan's Canon is clearly not without problems (Sober 2005). What is the "psychological scale"? Don't "higher" and "lower" assume the phylogenetic scale? In contemporary practice "lower" usually means associative learning, that is, classical and instrumental conditioning or untrained species-specific responses. "Higher" is reasoning, planning, insight, in short any cognitive process other than associative learning.

For an example of how Morgan's Canon might be applied today, suppose, contrary to the data in Figure 1.1, that crows had been found to drop nuts in front of cars more than on the empty road. An obvious "simple" explanation is that they had been reinforced more often when dropping a nut when a car was coming than when the road was empty and thereby had learned to discriminate these two situations. A "higher," anthropomorphic, explanation might be that having seen fallen nuts crushed by cars the insightful crows reasoned that they could drop the nuts themselves. The contrast between these explanations suggests a straightforward test: observe naïve crows to see if the discrimination between approaching cars and empty roads develops gradually (supporting the "simple" explanation) or appears suddenly, without any previous trial and error (supporting the "higher" explanation). Unfortunately, competing explanations do not always make such readily discriminable predictions about observable behavior. Even when they do, experiments designed to pit them against each other may not yield clear results. Then agnosticism may be the most defensible policy (Sober 2005).

In practice, the field of comparative cognition as it has developed in the past 30–40 years has a very strong bias in favor of "simple" mechanisms (Sober 2001; Wasserman and Zentall 2006a). The burden of proof is generally on anyone wishing to explain behavior in terms of processes other than associative learning and/or species-typical perceptual and response biases. To many, anthropomorphism is a dirty word in scientific study of animal cognition (Mitchell 2005; Wynne

2007a, 2007b). But dismissing anthropomorphism altogether is not necessarily the best way forward. "Anthropodenial" (de Waal 1999) may also be a sin. After all, if other species share common ancestors with us, then we share an a priori unspecifiable number of biological processes with any species one cares to name. Thus in some ways, as Morgan apparently thought (Sober 2005), the simplest account of any behavior is arguably the anthropomorphic one, that behavior analogous to ours is the product of a similar cognitive process. Note, however, that "simple" has shifted here from the cognitive process to the explanation (Karin-D'Arcy 2005), from "simpler for them" to "simpler for us" (Heyes 1998).

Where do these considerations leave Morgan's Canon? A reasonable modern interpretation of the Canon (Sober 2005) is that a bias in favor of simple associative explanations is justified because basic conditioning mechanisms are widespread in the animal kingdom, having been found in every animal, from worms and fruitflies to primates, in which they have been sought (Papini 2008). Thus they may be evolutionarily very old, present in species ancestral to all present-day animals and reflecting adaptations to universal causal regularities in the world and/or fundamental properties of neural circuits. As species diverged, other mechanisms may have become available on some branches of the evolutionary tree, and it might be said to be the job of comparative psychologists to understand their distribution (Papini 2002).

But for such a project to make sense, it must be clear what is meant by associative explanations and what their limits are. Associative learning, discussed in depth in Chapter 4, is basically the learning that results from experiencing contingencies, or predictive relationships, between events. At the theoretical level, such experience in Pavlovian (stimulus-stimulus) or instrumental (response-stimulus) conditioning has traditionally been thought of as strengthening excitatory or inhibitory connections between event representations. Thus one might say that any cognitive performance that does not result from experience of contingencies between events and/or cannot be explained in terms of excitatory and/or inhibitory connections is nonassociative. Path integration (Chapter 8) is one example: an animal moving in a winding path from home implicitly integrates distance and direction information into a vector leading straight home. As another, on one view of conditioning (Section 4.5.2) the flow of events in time is encoded as such and computed on to compare rates of food presentation during a signal and in its absence. Other nonassociative cognitive processes which might be (but rarely if ever have been) demonstrated in nonhumans include imitation, that is, storing a representation of an actor's behavior and later reproducing the behavior; insight; and any kind of reasoning or higher-order representations or computations on event representations. As we will see throughout the book, discriminating nonassociative "higher" processes from associative ones is

seldom straightforward, in part because the learning resulting from associative procedures may have subtle and interesting cognitive content. In any case, the goal of comparative research should be understanding the cognitive mechanisms underlying animal behavior in their full variety and complexity rather than partitioning them into rational or nonassociative vs. associative (Papineau and Heyes 2006).

In conclusion, neither blanket anthropomorphism nor complete anthropodenial is the answer (Mitchell 2005). Evolutionary continuity justifies anthropomorphism as a source of hypotheses. When it comes to comparing human cognition with that of other species, it is most likely that—just as with our genes and other physical characters—we will find some processes shared with many other species, some with only a few, and some that are uniquely human. One of the most exciting aspects of contemporary research on comparative cognition is the increasing detail and subtlety in our picture of how other species' minds are both like and not like ours.

1.3.3 Biological approaches to animal behavior

While experimental animal psychology was flourishing in North America, ethology was developing in departments of zoology in Europe (Burkhardt 2005). Guided by Tinbergen's four questions and the vision of developing a biological science of behavior distinct from psychology, ethologists emphasized the behavior of animals in the wild. They studied a wide range of species: insects, birds, and fish as well as mammals. Behavior was seen to be as much a characteristic of a given species as its coloration or the structure of its body (Lorenz 1941/1971; Tinbergen 1959). In an effort to break free of sentimental attitudes toward animals, ethologists emphasized the same objective behaviorist approach as Skinner and other experimental psychologists. For instance, at the very beginning of his textbook *The Study of Instinct* Tinbergen (1951, 4) warns, "Because subjective phenomena cannot be observed directly in animals it is idle either to claim or to deny their existence. Moreover to ascribe a causal function to something that is not observable often leads to false conclusions."

In the 1960s and 1970s the ethological study of the adaptive value and evolution of behavior developed into the field of behavioral ecology (Krebs and Davies 1993; Cuthill 2005). Behavioral ecology, or sociobiology (Wilson 1975), is characterized by an attempt to predict behavior from first principles of evolutionary biology using explicit models of the consequences of behavior for fitness. Like ethologists, behavioral ecologists focus on behavior of animals in the field and study a wide variety of species, but initially they were concerned almost exclusively with the functional and evolutionary "why" questions. Early research in behavioral ecology aimed to discover simply whether or not behavior had the properties predicted by evolutionary models. For example, did

redshank or some other bird choose food items optimally? As the field developed, and at about the same time as some psychologists (e.g., Kamil 1988; Shettleworth 1993) were advocating analyses of ecologically meaningful aspects of cognition, behavioral ecologists began to appreciate the role of cognitive mechanisms in producing or failing to produce the predicted behaviors (e.g., Stamps 1991; Huntingford 1993; Dukas 1998; Chittka and Thomson 2001). They began to ask, for example, about the processes of perception, learning, and choice that lead the redshank to select its prey and how these play a role in the bird's making, or failing to make, optimal choices (Chapter 11). The integration of cognitive psychology with the study of how animals solve ecologically important problems was referred to as *cognitive ecology* (Real 1993; Dukas 1998; Healy and Braithwaite 2000). *Sensory ecology* (Dusenbery 1992) and *neuroecology* (Bolhuis and Macphail 2001; Sherry 2006), were coined for the study of how sensory systems and brain architecture, respectively, are matched to species-specific environmental requirements.

1.3.4 Convergence and synthesis: Comparative cognition in the twenty-first century

Ethologists, behavioral ecologists, and traditional comparative psychologists emphasize different questions about animal behavior and tend to do their research in different settings and on different species, but their fields are clearly related. It stands to reason that data and theory of each of these fields should illuminate issues being studied by the others. Within psychology, this point of view led to what has been called the ecological or synthetic approach to comparative cognition (Kamil 1988; Shettleworth 1993). Unlike the anthropocentric or general process approach, the ecological approach emphasizes studying how animals use cognition in the wild, for example in foraging or finding their way around. Species are chosen on the basis of behavior indicating some particularly interesting cognitive processing such as the ability to home over long distances, use tools, keep track of relationships in a large social group, or remember the locations of large numbers of food items (Box 1.4). The ecological approach includes explicitly comparative studies designed to analyze the evolution and adaptive value of particular cognitive abilities. The species compared may be close relatives that face different cognitive demands in the wild and therefore are expected to have diverged in cognitive ability. Alternatively, species may be compared that are not very close relatives but face similar cognitive demands in the wild. Such species are expected to have converged in the ability of interest. Data about natural history and evolution are an integral part of this kind of comparative psychology, but so are theories and methods developed with the anthropocentric

approach. This approach is increasingly shared by biologists trying to understand cognitive processes underlying behaviors they observe in wild animals (e.g., Bluff et al. 2007; Cheney and Seyfarth 2007).

Cognitive ecology, sensory ecology, cognitive ethology, neuroecology, evolutionary psychology, ecological comparative psychology: whatever these enterprises are called, they all have in common the assumption that cognition is best understood by being studied in the context of evolution and ecology, that is, as a biological science. Together they have been converging into a vigorous interdisciplinary field of comparative cognition research. Kamil (1998) suggested that *cognitive ethology* should be reclaimed from those who use it to refer to studies of conscious processes in animals to refer to this synthetic research program. Reasonable though this suggestion may be, it does not seem to have been widely adopted (Allen 2004), and the term *comparative cognition* is generally used here. The present trend toward interdisciplinary research is a major departure from a century or more in which psychological research with animals (including often the human animal) has been largely divorced from, or even hostile to, the rest of the biological sciences and the framework provided by evolution (Richards 1987; Plotkin 2004). For more than 50 years, comparative psychologists (e.g., Beach 1950; Hodos and Campbell 1969) have been complaining about the detrimental effects of this divorce on psychological research with animals. Is the field itself evolving at last? There is plenty of evidence that it is. To some extent this evolution reflects the fact that psychology in general is becoming better integrated with the rest of the biological sciences, impelled by the apparent success of neuroscience and genetics in illuminating mechanistic underpinnings of behavior (e.g., Lickliter and Honeycutt 2003). But it also reflects the excitement generated by a variety of specific research programs that approach questions about animal cognition in a comprehensive biological framework.

Box 1.4 Food Storing Birds and the Ecological Approach

Some species of birds store food in the wild and use memory to find it again. One of the most remarkable is the Clark's nutcracker (*Nucifraga columbiana*) of the American Southwest (Figure B1.4). Nutcrackers bury thousands of caches of pinon pine seeds in the late summer and dig them up from beneath the snow throughout the winter and into the next spring (Balda and Kamil 2006). Early observers of food-storing in corvids (jays, crows, and nutcrackers) and parids (chickadees and titmice) found it incredible that these birds might be able to remember the locations of caches.

Perhaps they were just raising the general level of availability of food for all birds in the area. But food-storing would be unlikely to evolve unless the individuals doing it have greater fitness than lazy individuals which simply eat the food stored by others (Andersson and Krebs 1978). As this argument suggests, food storing birds do retrieve their own caches, and they use memory to do it (Shettleworth 1995).
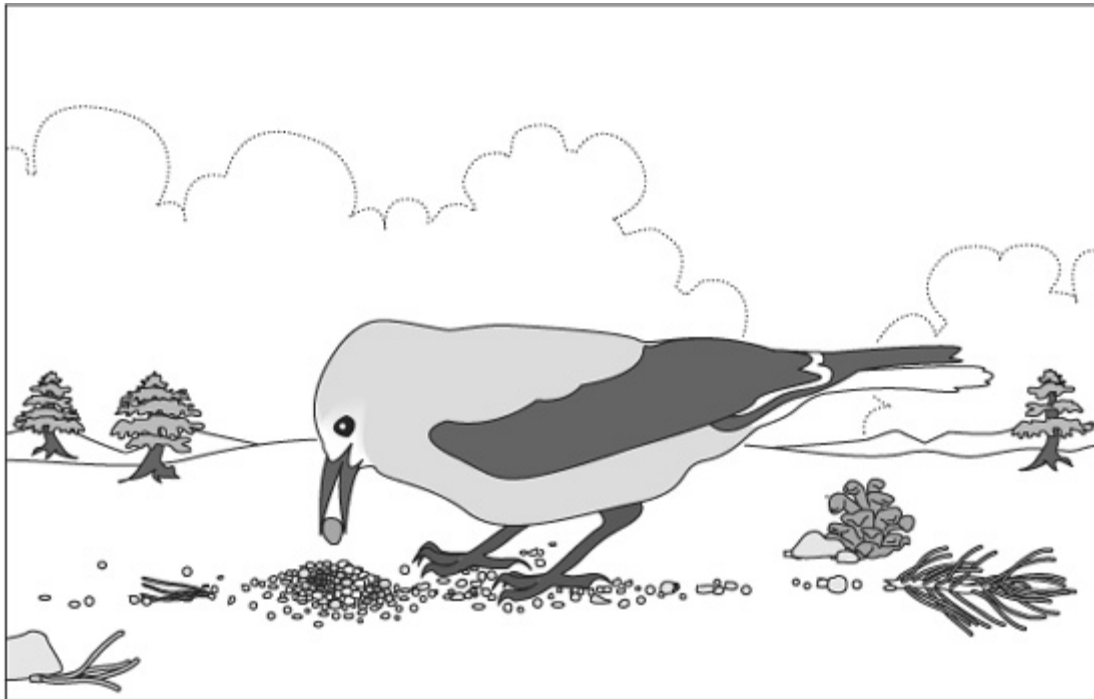

Figure B1.4. A Clark's nutcracker burying a seed. A bird generally caches several seeds in each site. From a photograph by R. P. Balda.

The fact that food-storers must remember the locations of a large number of items for days, weeks, or months suggests that along with the specialized behavior of caching food they may have evolved an enhancement of some aspect of memory. For example, maybe they can remember more items of spatial information for longer than other birds. Within both the corvids and the parids, some species store more food than others, so this hypothesis can be tested by comparing memory within each bird family. Corvids or parids that store more do tend to have better spatial memory, and the hippocampus, a part of the brain involved in spatial memory, is bigger relative to brain and body size in food storers than in nonstoring species. Both the data and the thinking behind these conclusions have proven controversial, as discussed in Chapter 2. Nevertheless, research on food-storing birds is still a good example of how information from evolutionary biology, field studies, neurobiology, psychological theories about memory, and techniques for testing memory in the laboratory can all be integrated to provide new insights.

For example, the last 20 years or so have seen the development of a lively cross-disciplinary field of research and theorizing on comparative social learning and possible precursors of human culture (Zentall and Galef 1988; Heyes and Galef 1996; Reader and Laland 2003; Galef and Heyes 2004; Richerson and Boyd 2005). Anthropocentrism has been turned on its head as studies of animal tool using, theory of mind, cultural transmission of skills, episodic memory and other capacities traditionally thought to be unique to humans are seen as relevant to understanding human cognitive evolution and development (e.g., Gomez 2005; Penn et al. 2008). The study of spatial behavior is increasingly interdisciplinary, embracing field and laboratory research on brain, behavior, and ecology of species as diverse as honeybees, ants, rats, and people (Gallistel 1990; Healy 1998; Jeffery 2003). Behavioral ecologists are embracing mechanistic studies at the level of the brain (Giraldeau 2004). Textbooks of animal behavior (e.g., Dugatkin 2004; Bolhuis and Giraldeau 2005) include sections on learning and animal cognition. The International Comparative Cognition Society, which began in 1994 as a small group of experimental psychologists mainly working with rats and pigeons, now represents researchers from psychology, biology, and anthropology studying most of the species and issues discussed in this book. As we see throughout the book, such convergence of researchers from different traditions, accustomed to focusing on different ones of Tinbergen's questions, can lead to misunderstanding and controversy, as when cognitive psychologists and behavioral ecologists disagree about what counts as *teaching* (Chapter 13), but it has also immeasurably broadened and enriched the field.

1.3.5 Comparative cognition and other areas of the behavioral and brain sciences

The comparative study of cognition intersects with many other areas of the behavioral and brain sciences. These include neuroscience, genetics, evolutionary psychology, developmental psychology, anthropology, conservation, and animal welfare. The research perhaps most closely connected to that discussed in this book concerns the neurobiological and molecular mechanisms of learning and cognition. By far the majority of studies of learning in animals at the present time are being done in this context (Domjan and Krause 2002). As Skinner wrote in *The Behavior of Organisms*, "a rigorous description at the level of behavior is necessary for the demonstration of a neurological correlate" (Skinner 1938, 422; Timberlake, Schaal, and Steinmetz 2005). So, for example, when researchers engineer a mouse strain that develops neurological symptoms of Alzheimer's disease (Chen 2000), deciding whether those mice show memory impairments analogous to those seen in human Alzheimer's sufferers depends crucially on having appropriate behavioral tests of memory, as well as knowledge of mouse behavior (Gerlai and Clayton 1999). Here, however, we will be

concerned with research on neuroscience and genetics only when it impinges on the understanding of cognitive processes as such.

Evolutionary psychology is also closely related to some topics in the present book. Evolutionary psychology is based on the premise that principles of cognition and behavior in humans are adaptations to social and environmental demands throughout evolution (Barkow, Cosmides, and Tooby 1992; Barrett, Dunbar, and Lycett 2002; Dunbar and Barrett 2007). For example, reasoning ability may have evolved at least in part to deal with social obligations in early hominid groups (Cosmides 1989). Evolutionary psychology has generated some controversial findings (see Buller 2005). One of its weak points is that its hypotheses often have to be based on conjectures about the conditions present early in human evolution. In this respect, research on the evolution of cognition in other animals is on much firmer ground because other species' present-day environments are likely much more representative of their past environments than is the case for humans. Hypotheses about evolution and adaptation can also be tested more directly in other species than in humans by comparing groups of present-day species. Thus research with nonhuman species can provide well-grounded hypotheses for testing in humans as well as a model for how such hypotheses should be tested (Daly and Wilson 1999). Indeed, the subject of this book might be described as evolutionary psychology "in the round" (i.e., in the broad sense, see Heyes 2000).

Some contemporary researchers directly address questions about the evolution of human cognition through studies with other species, for example seeking to combine insights from genetics, neurobiology, anthropology, child development, field studies of primate behavior, and laboratory tests to understand the fundamental question of what makes us different from even our closest living relatives, the chimpanzees and other primates (Chapter 15 and Gunter et al. 2005). This is particularly true in the study of spatial, numerical, and social cognition (Chapters 8, 10, and 12). Communication between comparative and developmental researchers is partly explained by the fact that those who study very young children share a problem faced by those studying animals—their subjects can't talk—making methods easily transferred between fields. It is also commonly assumed that any cognitive abilities chimpanzees share with us are most likely to be those shown by very young children (cf., Matsuzawa 2007).

Finally, the results of research on comparative cognition can have implications for conservation and animal welfare. For example, when members of an endangered species are raised in captivity to be released in the wild, it may be important to understand what they would have learned normally and figure out how to impart such knowledge to captive-reared individuals. This can include what predators to avoid (Griffin, Blumstein, and Evans 2000; Griffin 2004) and what cues indicate a

suitable habitat (Stamps and Swaisgood 2007). When it comes to animal welfare, there is a widespread sentiment that the more research shows that animals are like us, the more we should value and protect them (but see Wynne 2004b). Whatever one's point of view in this controversial area, knowledge about animal behavior and cognition can be applied to better understand and thus improve the welfare of both wild and captive animals (see Fraser and Weary 2005; Dawkins 2006).

1.4 Summary

Studying cognition means analyzing how animals acquire, process, and use information. Most people who study comparative cognition remain agnostic as to whether animals process information consciously or not. Some animals may be conscious in some sense, but we cannot know because consciousness refers to a private subjective state. Furthermore, it is often difficult to specify any behavior uniquely resulting from consciousness. How animals process information and behave adaptively can be understood, and on the whole should be studied, without reference to consciousness. Nevertheless, some researchers are of the opinion that some animals are undoubtedly conscious, and scientists should be trying to understand the nature of their conscious states.

Four questions, often referred to as Tinbergen's four whys, can be asked about any behavior. These are questions about immediate causation, development in the individual, present-day function, and evolution. The four questions are complementary; each contributes to a complete understanding of behavior. Cognitive mechanisms such as perception and memory are among the immediate causes of behavior; learning is part of behavioral development. Cognitive processes are also part of an animal's adaptation to its environment and therefore must have evolved through natural selection.

Cognition in nonhuman species has traditionally been approached differently by psychologists than by biologists. Psychologists have tended to take an anthropocentric approach, seeking to understand humanlike performance in other species and perhaps interpreting their findings by reference to an assumed phylogenetic scale. Anthropocentrism is not the same as anthropomorphism, or interpreting animal behavior as if it was caused by humanlike thought processes. Explicit anthropomorphism is thought to have been rejected with the adoption of Morgan's Canon early in the 1900s, but cannot be done away with entirely. The ecological or biological approach to cognition consists of analyzing the kinds of information processing animals do in situations of ecological importance like foraging, choosing mates, finding their way around. With this approach, species are compared with reference to evolutionary and ecological relationships. After a long history in which comparative psychology developed largely independently of biological studies of behavior,

contemporary research on comparative cognition is increasingly integrating these two approaches and making rich connections with other biological sciences.

Further reading and websites

The whole field of comparative cognition is covered in recent books including introductory texts by Wynne (2001) and Pearce (2008), the books edited by Balda, Pepperberg, and Kamil(1998); Heyes and Huber (2000); Wasserman and Zentall (2006b); and Bekoff, Allen, and Burghardt (2002), and the March, 2009, special issue of *Behavioural Processes* (vol. 80, no. 3). Hauser's (2000) *Wild Minds* and Wynne's (2004a) *Do Animals Think?* are excellent popular books by researchers in the field. Donald Griffin regularly updated his proposals about animal consciousness (Griffin 1976) almost until the end of his life (Griffin 2001). The animal behavior texts by Bolhuis and Giraldeau (2005) and Lucas and Simmons (2006) both cover topics included in this book, as does *Congnitive Ecology II* (Dukas and Ratcliffe, 2009). Papini's (2008) *Comparative Psychology* provides comprehensive background on the evolution of brain and behavior. *Behavioural Ecology* (Danchin, Giraldeau, and Cezilly 2008) is a comprehensive overview of that field.

From Darwin to Behaviorism (Boakes 1984) and the books by Richards (1987), Plotkin (2004), and especially Burkhardt (2005) are recommended for the history of thought and research in comparative psychology and ethology. *Tinbergen's Legacy* (Verhulst and Bolhuis 2009) reprints Tinbergen's 1963 paper along with the contemporary discussions of the four questions that were originally published in 2005 in *Animal Biology*. For animal consciousness, the writings of Dennett (1996), Allen and Bekoff (1997), Carruthers (e.g., 2005), and Sober (e.g., 2005) are useful; the chapter by Heyes (2008) is exceptionally clear on this and other issues. Kennedy's (1992) little book is a stimulating analysis of what he saw as the insidious influence of anthropomorphism. The discussions accompanying Wynne's (2007a) paper make clear that it is still controversial.

Most of the active scientists whose research is discussed in this book have lab websites with further information about their work. Many such websites and online editions of journals have links to video illustrations. These can be both entertaining and wonderful aids to understanding. The Animal Behavior Society and the Comparative Cognition Society both have comprehensive websites with links to researchers' sites, news, and events in the area. Given the ease with which these resources can be located, on the whole this book does not include specific references to online material.