Foraging

Behavior and Ecology

Edited by David W. Stephens,
Joel S. Brown, and
Ronald C. Ydenberg

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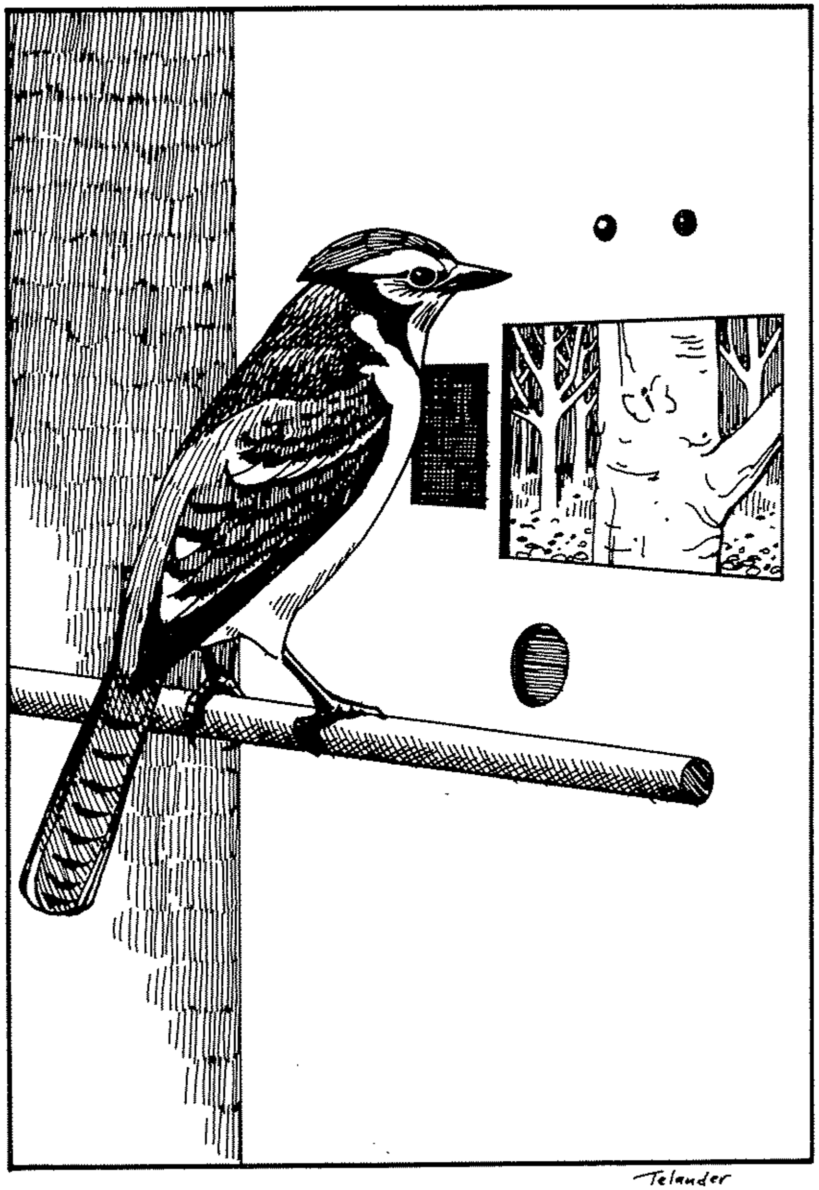


4

Cognition for Foraging

Melissa M. Adams-Hunt and Lucia F. Jacobs

4.1 Prologue

A hungry blue jay searches for prey along the branch of an oak tree. It scrutinizes the bark closely, ignoring the stream of noise and motion that occur around it. But when it hears a red-tailed hawk cry, it pauses and scans the scene. Seeing no threat, it resumes its search. Prey are difficult to find. Moths have camouflaged wings and orient their bodies to match the patterns of the bark. Dun-colored beetles press themselves into crevices. The jay peers at the bark, but does not immediately see any insects, even though they are within its field of view. Its gaze passes over several moths before it detects one outlined against the brown background. It catches and eats this moth. Renewing its search, the jay soon catches another moth, and then another. As the jay busies itself consuming moths, its gaze passes over many beetles, just as large and tasty, yet it does not detect them. Instead, the jay eats more moths, which it now finds easily, until only a few remain.

4.2 Introduction

An observer might wonder why the jay passes over valuable beetles. Answers to this question can take several forms. According to Tinbergen's classic framework, there are four levels of explanation: phylogeny, ontogeny, survival value, and mechanisms of foraging behavior (Tinbergen 1963). Cognitive scientists focus on mechanisms, the proximate causes of a behavior within the body of an organism. *Cognition* is the set of psychological mechanisms by which organisms obtain, maintain, and act on information about the world. Broadly, these mechanisms include perception, attention, learning, memory, and reasoning. Although humans experience some cognition consciously (but much less than it seems to us; see Kihlstrom 1987), researchers can usually study the information processing aspects of a cognitive process without knowing whether it is conscious. This becomes important when studying nonhumans because we cannot ask them about their conscious cognition. In our prologue, the blue jay's cognitive processing (conscious or not) determines which cryptic prey it will detect, as we will describe in more detail later.

Cognition enables foragers to identify and exploit patterns in the environment, such as by recognizing objects—whether prey, conspecifics, or landmarks—and predicting their future behavior. Evidence suggests that cognitive abilities can affect fitness and evolve (Dukas 2004a). Reasonably, these abilities may have become crucial for survival and reproduction, evolving as their enhancement led to greater fitness. Learning and memory may also have allowed animals to colonize new ecological niches, leading to new selection pressures on their cognitive abilities. Cognition, ecology, and evolutionary processes are intimately connected. This realization has led to a new interest in the role of cognition in understanding species' behavioral ecology and hence to biologists and psychologists collaborating on comparative studies of cognition (Kamil 1994).

Many fields, including ethology, behavioral ecology, comparative psychology, anthropology, neuroethology, cognitive science, and comparative physiology, have informed the study of cognitive processes in nonhuman species. This chapter introduces some of the major phenomena and issues in cognition and foraging research, outlining their diversity and complexity. It discusses four functional problems faced by a forager: perceiving the environment, learning and remembering food types, locating food resources, and extracting food items once found.

4.3 Perceiving the Foraging Environment

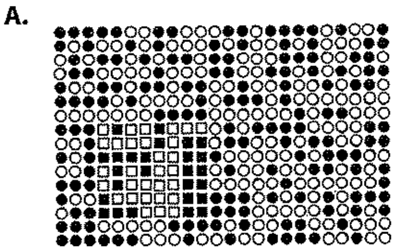
Perception begins with sensation: the conversion (*transduction*) of environmental energy into a biological signal (usually neural) that preserves relevant patterns (*information*). When light from the moth and its substratum activates

the jay's photoreceptors, the jay senses the moth. The range of sensory abilities among species is impressive, even within taxonomic groups. For example, the auditory sensitivity of placental mammals ranges from the infrasonic vocalizations of elephants to the ultrasonic calls of bats. Diverse sensory modalities exist, including chemo-, electro- and magnetosenses. Animals may also have internal sensations such as proprioception, pain, and hunger. As a consequence of this diversity, the *Umwelt*, or "sensory world" (von Uexküll 1957), of any species is not easily accessible to others—an important realization for humans who study nonhumans. From the available stream of sensory information, an individual must select what is relevant to its current goals. Our jay, for instance, needs to find its prey, the moth.

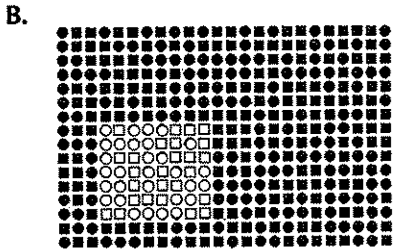
Feature Integration

To perceive the moth, the jay must separate the moth from the background. This task can involve several cognitive mechanisms. For example, if a mottled white moth rests on a brown oak tree, the jay will immediately perceive the moth by its color, regardless of how closely its texture matches the substratum. Perception researchers call this the *pop-out effect* because under these circumstances items seem to "pop out" from the background. Feature integration theory provides a basic framework for understanding this effect. According to this theory, the visual system treats each perceptual dimension, such as color or line orientation, separately. If a target (the item being searched for) differs from its surroundings in one perceptual dimension, it pops out. When the target lacks a unique feature, pop-out does not occur, and a forager must search more carefully, as when a jay searches for a cryptic moth. In such a *conjunctive search*, the forager must inspect items that share features with the target (*distractors*) one at a time. This necessity decreases search performance linearly. When pop-out occurs, the search, called a *feature search*, proceeds simultaneously on all dimensions. *Attention*—the focusing of limited information processing capacity—is needed in a conjunctive search to *bind* (integrate) separate dimensions, while pop-out occurs without attention (Treisman and Gelade 1980).

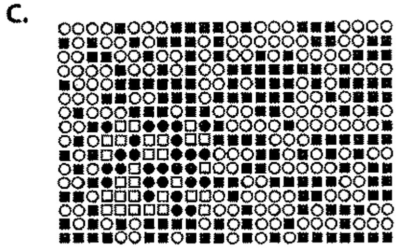
Texture segregation experiments with both humans (Treisman and Gelade 1980) and pigeons (Cook 1992) fit this model of feature integration. Displays of small shapes varying in color (e.g., black or white squares and circles), within which a configuration of the small shapes formed a rectangle, were used in one such experiment (fig. 4.1). In the feature search condition, the rectangle contained either all the same shape or all the same color. In the conjunctive search condition, the rectangle contained both shapes, oppositely colored,



Feature - Shape



Feature - Color



Conjunction - Color and Shape

Figure 4.1. Stimuli used to study texture segregation. Subjects search for a target (the small rectangle) within the display. Displays A and B illustrate targets that differ in a single feature (shape or color) from the background. Note the "pop-out" effect for these single-feature displays. Display C contains a target that differs from the background in a conjunction of features: black circles and white squares in a background of white circles and black squares. Note the difficulty in locating this target. Both pigeons and humans show decrements in performance on such conjunctive searches. (After Cook 1992.)

and the background contained the two remaining combinations. Both humans and pigeons performed poorly in conjunctive searches. Another visual search experiment (Blough 1992) found evidence of serial processing during conjunctive searching in pigeons. Blough used alphanumeric characters as distractors and the letter "B" and a solid heart shape as targets. The number of distractors did not affect search time for the dissimilar heart shape, but increased search time for the cryptic letter "B." Together, these studies suggest that in pigeons and humans, two disparate species that rely on vision, integration of features may require attention. Challenges and extensions to this theory are reviewed in Palmer (1999) and, with additional pigeon experiments, in *Avian Visual Cognition* (see section 4.8 for URL).

Search Image

Luuk Tinbergen (1960) observed great tits in the field delivering insect prey to their young and compared these observations with changing abundances of prey. When a new prey species became available, Tinbergen found that parents collected it at a low rate for a while before the collection rate caught up to its abundance. Tinbergen interpreted this pattern as revealing a cognitive constraint on search: the food-collecting parents behave as if they are temporarily "blind" to the abundance of a newly emerged prey type. He argued that foraging animals form a perceptual template of prey items over time. We now call this phenomenon *search image*.

Laboratory studies have shown that search image effects occur only when prey are cryptic (Langley et al. 1996), suggesting that animals require search images only for conjunctive searching. As reviewed by Shettleworth (1998; see also Bond and Kamil 1999), search image is probably an attentional phenomenon that selectively amplifies certain features relative to others. *Sequential priming* may be the mechanism involved. Every time a predator encounters a feature (e.g., a blue jay encounters the curved line of a moth wing), the perceptual system becomes partially activated (*primed*) for that feature. Priming is a preattentive process that temporarily activates a cognitive representation, often facilitating perception and attracting attention. A classic study by Pietrewicz and Kamil (1979) of blue jays searching projected images for cryptic moths supports the role of sequential priming in search image formation. In these experiments, jays saw photographs of *Catocala relicta* (a light-colored moth) on a light birch background, *C. retecta* (a dark-colored moth) on a dark oak background, and pictures of both types of tree bark with no moth. The apparatus rewarded the jays with a mealworm for pecking at pictures that contained moths. The birds' ability to detect a single moth species improved with consecutive experiences, consistent with sequential priming. Mixing two prey types in a series blocked the improvement.

Bond and Kamil (1998) showed that this search image effect can select for prey polymorphisms because search image formation lags changes in the relative frequency of morphs. The experimental predators, again blue jays in an operant chamber, generated frequency-dependent selection that maintained three prey morphs in a population of digitized images. Jay predation selects for both polymorphisms and crypticity in moths, which may fuel the evolution of the jay's perceptual capacities in turn (Bond and Kamil 2002).

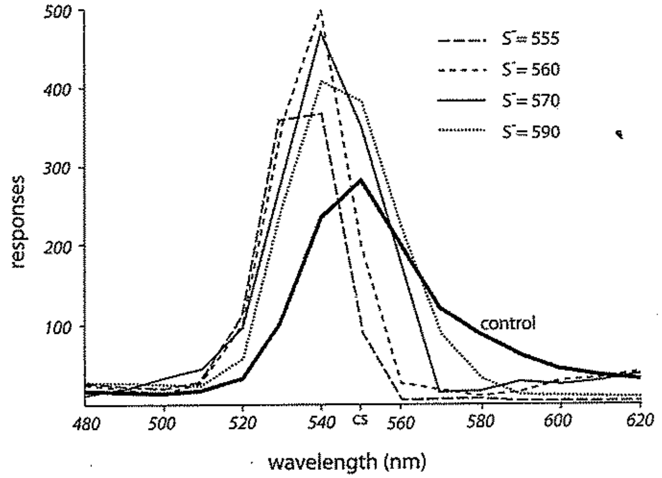


Figure 4.2. Stimulus generalization to a light with a wavelength of 550 nm (the conditioned stimulus, or CS) with no discrimination training and with training to avoid a light of greater wavelength (S^-). Pigeons trained to respond only to the CS (control) showed a peak response (highest number of pecks) to wavelengths very near the CS. Note the "peak shift" effect caused by discrimination training: the peak response moves away from the negatively trained stimulus. (After Hanson 1959.)

Stimulus Generalization

Because no two moths are identical, the foraging jay must generalize. Stimulus generalization allows a forager to discount minor differences in stimuli. In a classic study, Hanson (1959) trained pigeons to peck at a key that emitted light at 550 nm, a greenish yellow color. When presented with random wavelengths, the trained pigeons also responded to wavelengths close to 550 nm and less strongly to wavelengths farther away (fig. 4.2).

An important characteristic of stimulus generalization is its flexibility. Discrimination training can shift the response peak away from a trained stimulus. When Hanson further trained groups of pigeons to inhibit their response to a second wavelength greater than 550 nm, the pigeons preferred wavelengths less than 550 nm (see fig. 4.2). This *peak shift* effect shows the flexibility of stimulus generalization, which allows animals to group similar stimuli according to behavioral requirements or experience. Peak shift has been shown in animals from goldfish to humans (see Ghirlanda and Enquist 2003 for a review of stimulus generalization).

Categorization

Stimulus generalization may underlie some categorizations. Wasserman and colleagues used a sorting task to investigate visual categorization in pigeons. First, they trained pigeons to match four classes of objects (cats or people, cars, chairs, and flowers) with the positions of four pecking keys (left or right, upper or lower), where each key corresponded to one object class. Intermittently during training with one set of drawings, the experimenters tested the pigeons with a set of new images from these object classes. This testing demonstrated that the pigeons had not simply memorized the correct response for each image, but were generalizing (Bhatt et al. 1988). In a further demonstration, Wasserman and colleagues required pigeons to sort these same images into "pseudocategories" (classes with an equal number of cats, flowers, cars, and chairs). This greatly impaired the pigeons' performance, suggesting that categorization underlies this behavior (Wasserman et al. 1988). Although this result shows that pigeons can use visual criteria to categorize pictures, because all car drawings resemble one another in many ways, we cannot eliminate an explanation based on stimulus generalization.

To eliminate stimulus generalization, Wasserman and colleagues performed a three-stage experiment. In stage 1, they created superordinate categories of perceptually dissimilar objects. One group of pigeons learned to peck at a key near the upper right corner of a screen if they saw a person or a flower and to peck at a key near the lower left corner if they saw a chair or a car (fig. 4.3). In stage 2, the experimenters changed the response required for each category. The pigeons above saw only people or chairs. When the apparatus showed images of people, the pigeons had to peck the key at the *upper left*. Similarly, when the screen showed images of chairs, the pigeons had to peck the key at the *lower right*. What happened when these pigeons saw flowers again in stage 3? Did they peck at the upper left because that was the correct response for the person-flower category in stage 2, or did they choose between the two new responses randomly? On 72% of stage 3 trials, pigeons in this experiment chose the key corresponding to their category training in stage 2 (e.g., upper left key for flowers and lower right key for cars) (Wasserman et al. 1992). This result demonstrates that pigeons can form a *functional equivalence* between perceptually dissimilar items, a characteristic of true categorization (see Khallad 2004 for review).

Do animals have natural functional categories? Watanabe (1993) trained one set of pigeons to group stimuli into food versus nonfood categories and another set of pigeons to group stimuli into arbitrary categories (with equal numbers of food and nonfood items). Watanabe also trained some individuals with real objects and others with photographs. After training, the experimenter tested subjects on transfer to the opposite condition (real objects to photographs and photographs to real objects). The pigeons trained to distinguish food from nonfood easily transferred their skills from one type of stimulus to the other, but those trained with arbitrary categories did not transfer their skill.

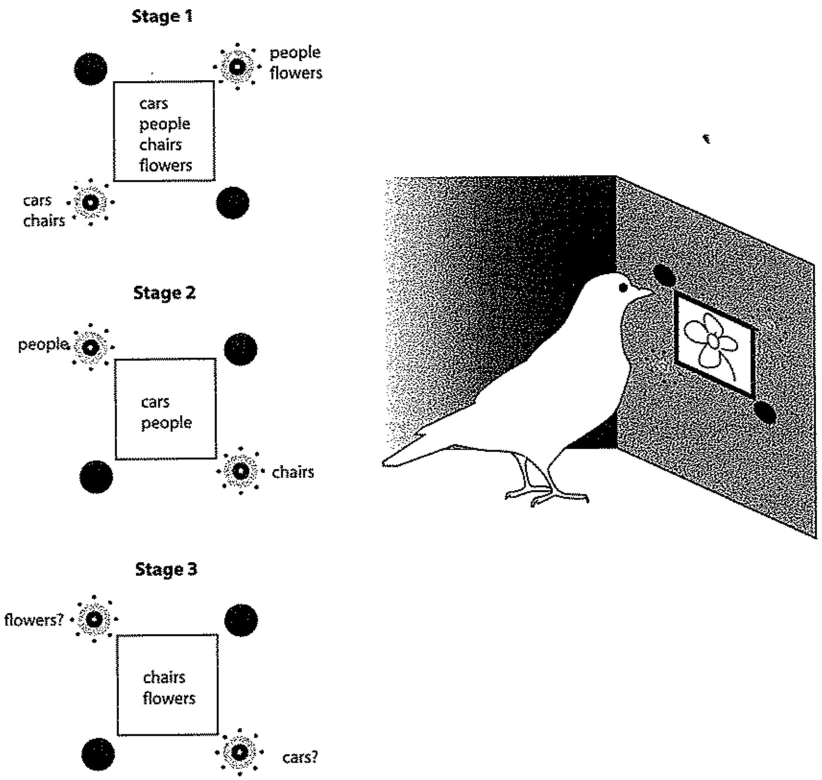


Figure 4.3. Testing for categorization in pigeons using an operant chamber. Subjects pecked at one of two illuminated keys (open circles) in response to a photographic stimulus (listed inside the square) to receive a reward. Correct answers and predicted responses are indicated beside the keys. In stage 1, subjects learned to make a common response to perceptually different pairs of stimuli (cars and chairs or people and flowers). In stage 2, subjects learned a new response for one type of stimulus in each pair. Stage 3 tested whether subjects would generalize this new response to the other stimulus type (cars or flowers). (Experimental design from Wasserman et al. 1992.)

This finding suggests that the subjects in the food/nonfood condition used categories, but those in the arbitrary category condition were making memorized responses to particular stimuli. Moreover, Bovet and Vauclair (1998) found that baboons could categorize both objects and pictures of those objects into food and nonfood groups after only one training trial. Functional categorization is another type of generalization. A forager that can parse its world into groups of related objects can recognize the properties of novel exemplars and predict how they will behave.

Quantity

After determining what objects are around, a forager may need to process information about quantity: How many moths did I encounter in that patch? How many individuals are in my group? An animal might use any of several methods to solve problems about quantity. Detecting *relative numerousness* is simply determining that one set contains more than another. Several species can use relative numerousness to make judgments about quantity, including laboratory rats, pigeons, and monkeys (see discussion in Roberts 1998). In contrast, to discriminate absolute number, the animal must perceive, for example, that four stimuli differ from three and five. Davis and colleagues have demonstrated that laboratory rats can discriminate the absolute number of bursts of white noise, brushes on their whiskers, wooden boxes in an array, and even the number of food items they have eaten (Davis 1996).

How animals accomplish such feats has been the subject of considerable debate. Humans can *subitize*, or perceive the size of small groups of items that are presented for less time than would be needed to count them. Subitizing may be a perceptual process in which certain small numbers are recognized by their typical patterns (or rhythms in the case of nonvisual stimuli). Humans subitize so quickly that the process appears to be preattentive. Animals may subitize, but there is also evidence that they count. Alex, an African gray parrot, could identify the number of objects (wood or chalk pieces, colored orange or purple) by color and/or material on command (Pepperberg 1994). Since selecting the objects to count involves a conjunction of shape and color, Alex may have to count each item serially. Capaldi and Miller (1988) argue that laboratory rats automatically count the number of times they traverse a runway to obtain food because they behave as if they expect reward after a certain number of runs, whether they travel the runway quickly or slowly. This number expectation was transferred when the investigators changed the type of reward, suggesting that rats count using abstract representations rather than specific qualities of the reinforcer. Notwithstanding these impressive numerical feats, some researchers are not ready to conclude that nonhumans meet the strict standard of counting in which each item in a list has a unique tag or identifier (see Roberts 1998 for discussion).

Synopsis

Cognition begins with sensation and perception. Animals possess diverse senses, such as vision, audition, touch, electroception, and proprioception, which provide the information an animal needs to forage effectively. Attention binds complex conjunctions of sensory information. Search image results from these perceptual and attentional processes. Stimulus generalization allows an animal to group stimuli based on sensory similarity. Categorization allows animals to group objects functionally. Finally, numerical competencies allow animals to quantify food items. These processes enable the forager to perceive its environment.

4.4 Learning What to Eat

If a new prey item replaces an old one, a jay that can learn to eat this new prey will be more successful. We will define learning as a change in cognition caused by new information—not by fatigue, hunger, or maturation, which can also cause cognitive changes. Learning has no adaptive value when the environment is completely static or completely random, since learned information cannot be applied (Stephens 1991). In the appropriate environment, learning allows adaptation to occur on an ontogenetic time scale rather than a phylogenetic one. Learning is related to memory: learning is a *change* in information processing, while memory is the *maintenance* of an information state. In practice, students of learning and memory find it difficult to distinguish the two. A forager must, in the end, both learn what to eat and remember what it has learned.

Classical Conditioning

An experienced blue jay may form an association between the shape of a moth and food or between shaking a branch and the appearance of this food item. Known as *associative learning* or *conditioning*, the formation of associations plays an important role in behavior. Classical or Pavlovian conditioning involves passive associations (as in the first case), while instrumental or operant conditioning (which we will discuss later) involves associations between the animal's own behavior and its results. In classical conditioning, the animal learns that something that had been neutral (the conditioned stimulus, or *CS*; e.g., moth shape) seems to appear predictably with something that it has an innate interest in (the unconditioned stimulus, or *US*; e.g., food) and to which it will make an innate response (the unconditioned response, or *UR*; e.g., salivation in the case of Pavlov's original experiments with dogs). Based on this relationship, simply perceiving the conditioned stimulus leads to a response, called the conditioned response (*CR*), which is often identical to the UR. Common conditioning procedures are described in box 4.1. Modern conditioning researchers generally consider the mechanism underlying the CR to be a cognitive representation of *expectancy*, rather than the Pavlovian "reflex." These researchers also recognize that all traditional conditioning phenomena may not be explainable by one mechanism, and they acknowledge alternative forms of learning, such as learning by observation, which we will discuss below (see Kirsch et al. 2004 and Rescorla 1988 for excellent discussions).

BOX 4.1 Learning in the Laboratory

Researchers studying learning in the laboratory have developed many standard procedures and uncovered numerous replicable phenomena. Here we review some of the best known of these phenomena.

Second-Order Conditioning

A blue jay learns that a rainfall precedes wet leaves, which in turn predict greater abundance of certain invertebrates. Soon, rain by itself will stimulate the jay to look for those prey species. In the laboratory, we first condition a hungry rat to expect food (US) when we switch on a light (CS_1). Then we pair the light with a tone (CS_2), and soon the tone by itself will come to elicit salivation (CR). The conditioning to the tone is second-order conditioning. We have, in effect, chained two conditioned stimuli together.

Conditioned Inhibition

A blue jay that has learned to hunt brown moths on oak trees now learns a new association—that the presence of another blue jay on the same tree is almost always correlated with an absence of moths. This association causes conditioned inhibition of its foraging response. Conditioned inhibition occurs when we pair a CS, such as a tone, with the US (e.g., food) only when the CS appears alone, but not when it appears with a second stimulus, such as a light. This experience inhibits the response to the light-tone combination. Conditioned inhibition allows the forager to learn the circumstances in which a CS (oak tree) does not signal the US (moth).

Sensory Preconditioning

A blue jay encounters an orange butterfly resting on a clump of moss, but sated, it flies away. Later, the blue jay learns that the orange butterfly is toxic. Afterward, the blue jay may show a withdrawal response to the moss, even in the absence of the butterfly. In the laboratory, we present two CSs (such as a light and a tone) together prior to any conditioning procedure. When later, we pair one of these (e.g., the tone) with a US (e.g.,

(Box 4.1 continued)

food) in a conditioning procedure, the second one will also elicit the CR (e.g., salivation) with no direct training. Though this phenomenon seems similar to second-order conditioning, it is actually a form of *latent learning* in which animals gain information (such as an association) in the absence of any apparent immediate benefit for doing so.

Blocking

A blue jay searches for acorns in an oak tree. Every time it finds a branch of a certain diameter, the branch also contains many acorns. It then searches out branches of that diameter. However, on the other side of the tree, branches of this diameter are also covered with lichens. A second blue jay happens to find many acorns on this side, and learns to search for branches of a certain diameter that are covered with lichens. The first blue jay, when it then moves into the lichen area, does not learn that lichens predict acorns. In the laboratory, we condition a subject by pairing a tone with food until the tone reliably produces salivation. After we have completed this conditioning, we present a compound stimulus made up of our old tone and a new light. When we test the subject with the light and tone separately, we find that the tone produces salivation as before, but the light has no effect. We say that the prior conditioning to the tone blocks conditioning to the light. Psychologists view blocking as an important conditioning phenomenon because it demonstrates that correlation with the US is not sufficient for learning to occur; after all, the light has been correlated with food, so one might expect salivation to the light as well, but this is not what we find. Blocking suggests an information model of conditioning: the second CS (the light) adds no new information because the first CS (tone) already perfectly predicts the US (food).

Overshadowing

A blue jay learns that orange wings predict toxicity in butterflies. Black spots also predict toxicity, but the jay has not learned this. In the laboratory, we begin such a conditioning experiment by pairing a compound light-tone stimulus with food until our compound stimulus reliably produces salivation. When we test the light and tone separately, we typically find that one stimulus elicits salivation much more strongly. If we find that the tone and not the light elicits salivation, then we say that the tone overshadows the light. If the light and the tone differ greatly in intensity, size, or saliency (as with a dim light and a loud tone), it is the larger, brighter, louder, or more

(Box 4.1 continued)

critical CS that gains the most strength in eliciting the CR. Studies suggest that subjects learn both CSs, but not equally well. Biological relevance, as found in the Garcia effect (see section 4.4), can be a cause of overshadowing.

Latent Inhibition

A blue jay searching for food never finds any at its nest tree. One morning an infestation of bark beetles takes hold in the tree. The blue jay sees one, but does not stay to forage at the tree. In fact, it takes the jay quite a while to learn that its own tree is now a source of food. In the laboratory, we play a tone to an experimental subject. The subject hears the tone frequently, but it is not correlated with food or other salient events in the subject's environment. If we then try to condition the subject by pairing the tone with food, we find that this prior exposure to an irrelevant tone inhibits conditioning. It is as if what has been learned (that the tone predicts nothing and therefore can be ignored) must be unlearned before the new association can be made. Latent inhibition supports an information model of conditioning and contradicts the expectation that familiarity would facilitate learning.

Extinction

A blue jay foraging for acorns on a particular tree always finds an acorn when it searches in that tree. As the season progresses, the jay is less likely to find an acorn. Eventually, the tree is empty. At the same time, the blue jay becomes less likely to search that tree. In the laboratory, we pair a light with food until a rat reliably presses a lever to get food when the light appears. Now we begin to switch on the light without food. Over subsequent trials, the rat no longer responds to the light. The stimulus that used to provide information about the arrival of food is now useless, and the subject stops responding to it. Like latent inhibition, extinction involves learning not to respond to an unpredictive CS. Psychologists often use the speed of extinction to measure the strength of the original association.

Conditioning Mechanisms

Kamin (1969) first suggested that surprise might cause a new association to form. He proposed that when unexpected events occur, the startle response stimulates an animal to learn. An expected event, in which one stimulus already predicts the occurrence of another, does not facilitate learning, as the blocking phenomenon (see box 4.1) demonstrates. Rescorla and Wagner

(1972) formalized this idea in an elegant model, $\Delta V = \alpha\beta(\lambda - V)$. The term ΔV represents the change in associative value (learning) during a trial. The constants α and β signify the salience of the CS and US, respectively. The difference $(\lambda - V)$ represents the maximum associative strength that the US can support (λ) minus the current associative value of all CSs (V). Behavioral psychologists call the difference $(\lambda - V)$ unexpectedness. Thus, no learning occurs when an animal expects an event [e.g., when $(\lambda - V) = 0$], but learning proceeds quickly when an event is unexpected [$(\lambda - V)$ is large]. This model correctly predicts a negatively accelerated learning curve and also predicts several conditioning phenomena, including the blocking effect. Yet even this influential model cannot explain all standard conditioning phenomena, and theories continue to be developed (see Kraemer and Spear 1993; Miller and Escobar 2001; and other reviews in Zentall 1993).

Ecology and Conditioning

For years, experiments seemed to show that conditioning was equally likely with any arbitrary stimulus—a phenomenon known as "equipotentiality." In 1966, a classic experiment on what became known as "taste aversion" or the "Garcia effect" challenged this dogma. Garcia and Koelling (1966) trained rats to drink saccharine-flavored water while lights flashed and a nearby speaker clicked. This procedure made three neutral stimuli available for conditioning (taste, sound, light). Next, they gave one group mild electric shocks on the feet while they were drinking and made another group nauseated by giving lithium chloride injections or by X-ray exposure several hours later. They then offered each group a choice between flavored water and water near flashing lights and clicking sounds. The shocked and nauseated groups made different choices. Rats from the shocked group avoided the water with lights and noise, but drank the flavored water readily. Rats from the nauseated group avoided the flavored water, but drank the water with lights and noise. This finding demonstrated that the effectiveness of a CS is influenced by its natural relationship to the US. These procedures also violated prevailing wisdom in producing learning after one trial, rather than gradually, and association between events occurring across a long temporal gap (see historical review in Roberts 1998).

Conditioning had also been believed to be the same across species, or universal. Rats are nocturnal foragers that collect and transmit information about what is good to eat via chemical cues, such as a novel odor in the breath of a colony member (Galef 1991). It makes sense that they would associate nausea with a novel flavor, rather than with a food that looked or sounded different. If conditioning effects are adapted to ecological niches, then a visual forager might show the opposite pattern. Exactly this result was found in Japanese quail. Wilcoxon et al. (1971) found that quail could associate the color blue with later nausea.

Aposematic (or warning) coloration trains visual predators more quickly than less intense coloration. First, they see the prey more quickly (the pop-out effect) and learn about them more quickly. In the laboratory, chicks learn to avoid bad-tasting, brightly colored prey more quickly than similar prey that are cryptic (Gittleman and Harvey 1980). But the lessons from cognitive science for the forager do not stop there. These preferences may be transmitted to conspecifics by observation. Day-old chicks (reviewed in Nicol 2004), red-winged blackbirds, and cotton-top tamarins (reviewed in Galef 2004) learn to avoid foods by observing the negative responses of conspecifics. Furthermore, stimulus generalization makes it possible for predators to avoid any species that resembles a poisonous species. This cognitive process underlies the evolution of mimicry, both when the mimic species is palatable (Batesian mimicry) and when it is toxic (Müllerian mimicry, reviewed in Goodenough et al. 1993).

Memory

The blue jay that learns about a new moth species must also remember this information. Memory can be categorized by different characteristics: duration — (long-term vs. short-term), content (episodic, semantic, procedural), use (working memory), or conscious access (declarative memory). Animal cognition researchers commonly recognize three basic types of memory (cf. Roberts 1998 and Shettleworth 1998). *Working memory* is short-term and used within the context of a foraging bout. A blue jay, for example, uses working memory to keep track of which branches it has already searched and to avoid them. *Reference memory* is long-term and is used for other information: where the jay is located in space, where the important resources are, the concept that a moth is food, the rules it has extracted about foraging for moths in that area, and so forth. Finally, there is *procedural memory* of specific skills, such as the movements needed to handle a particular prey species. More fine-grained categories include spatial and serial memory.

Organizing Memories

Animals may organize their memories into *chunks*, smaller lists that are organized categorically, such as places where white moths were found versus places where brown moths were found. Pigeons in an operant chamber learning to peck unique keys in a certain order will learn the task more quickly if the first few keys differ by color (the colored chunk) and the remaining keys differ by pattern (the patterned chunk), or vice versa. When the colored and patterned keys are intermixed, pigeons do not perform as accurately (see reviews in Roberts 1998). The same thing happens with the organization of spatial information: things that are similar are chunked together in memory. For example, rats foraging for three types of food in a twelve-arm radial-arm maze organize their search to retrieve the items in order of preference. If the three types are always found in the same places in the maze, even if these locations are scattered across the maze, the rats become very efficient at increasing their "chunk size," the number of objects of the same type taken in a run. They also learn the twelve arms of the maze more quickly than a second group of rats for which the three food types are placed in random locations in the maze on each trial. The rats therefore seem to categorize the twelve foraging locations (i.e., the ends of the maze arms) by the type of food each contains, and their ability to search proficiently (i.e., one visit to each arm) depends on this ability to organize their memories in this way (Dallal and Meck 1990). Similarly, a blue jay may categorize foraging sites by the prey found there and use this information to organize its foraging routes.

Interference between Memories

If a blue jay first learns about moths on one tree and then about caterpillars on a second tree, the memory of the caterpillars may interfere with the memory of the months. This example illustrates *retroactive* interference, in which a more recent memory interferes with an older one; however, *proactive* interference (in which the moths interfere with the caterpillars) also occurs. Interference occurs at both short and long intervals and thus affects both working and reference memory. For example, pigeons performing delayed matching-to-sample working memory tasks showed both proactive and retroactive interference. In the first task, the experimenter trained pigeons to peck a red key if they saw a red sample stimulus before the delay and a green key if they saw a green sample stimulus. Showing a light of the wrong color before the sample (e.g., green before a red sample) impaired recall in the test phase. Manipulating the interval between the interfering stimulus and the sample changed the degree of proactive interference, demonstrating that competition for encoding does cause proactive interference. Also in a delayed matching-to-sample task, adding distracting stimuli to the interval between sample and test reduced performance and demonstrated retroactive interference (see Roberts 1998).

Maintaining Working Memory

While foraging, the blue jay may need to keep in mind what it is looking for or where it has already looked. This is the role of working memory, which actively filters and prioritizes current data. Active cognitive processes can influence the strength of a memory, increasing it through *rehearsal* or decreasing it through *directed forgetting*. Rehearsal is mentally repeating an event or stimulus (e.g., repeating a phone number), improving memory for that item. Directed forgetting actively decreases or represses working memory for information deemed irrelevant. These two processes may be interrelated.

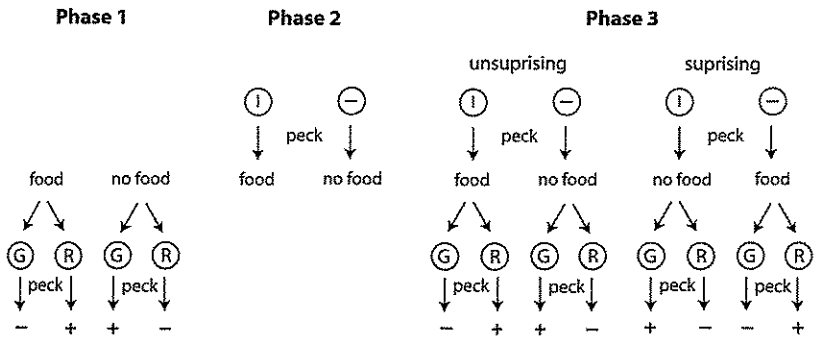


Figure 4.4. Testing for rehearsal in working memory. Pigeons in an operant chamber received the three phases of training diagramed here. Circles represent stimuli on keys: green (G), red (R), vertical line, or horizontal line. + or − indicates reward or no reward. Note that the only difference between the unsurprising and surprising test groups in phase 3 is whether pecking the lined keys resulted in food or no food as expected. (Experimental design from Maki 1979.)

Studies have demonstrated both rehearsal and directed forgetting in pigeons (see reviews in Roberts 1998). Maki (1979) demonstrated rehearsal using a complicated three-phase delayed symbolic matching-to-sample task (fig. 4.4). In phase 1, the sample stimulus was either the presence or absence of food. In the presence of food, the pigeon had to peck a red key (the "symbolic" match for the food stimulus) to obtain a reinforcement. In the absence of food, a green key resulted in reinforcement. In phase 2, there was no matching, only a contingency. Here pigeons learned that if a vertical line was presented, they would receive food, but if a horizontal line was presented, they would not. Maki divided his phase 3 tests into two types of trials, "surprising" and "unsurprising." During unsurprising trials, the apparatus first showed one of the line stimuli (vertical or horizontal), and then the event the pigeons had come to expect (food or no food, respectively) ensued. Maki then used this event (food or no food) as the sample stimulus for a delayed symbolic matching-to-sample task identical to that in phase 1. In surprising trials, the apparatus showed the line stimuli (vertical or horizontal) as before, but the experimenter switched consequences (no food or food, respectively). As in the unsurprising treatment, Maki then tested the pigeon's memory of the food/no food event using a delayed symbolic matching-to-sample task identical to that in phase 1. "Surprised" pigeons showed better recall. If we assume that surprised pigeons spend more time "mulling over" their surprising observations, then this finding suggests a role for rehearsal in nonhuman memory. Using an entirely

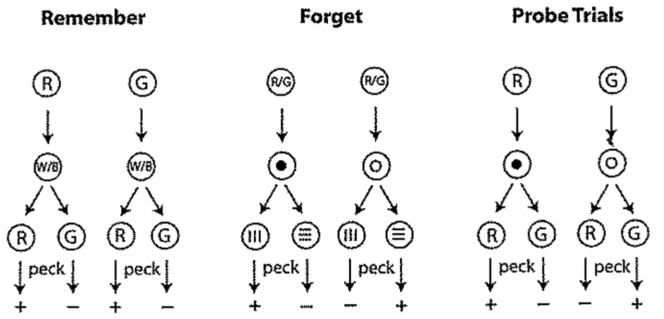


Figure 4.5. Testing for directed forgetting in pigeons. Following a white or blue stimulus (W/B, "remember cues"), pigeons received a memory test for the previous stimulus (G, green, or R, red). Following dot stimuli (solid or open dots, "forget cues"), pigeons received a symbolic matching-to-sample memory test for the dot stimulus: solid dot matches vertical lines, open dot matches horizontal lines. In probe trials, horizontal or vertical lines were replaced with a red/green memory test for the previous stimulus. + or − indicates reward or no reward. (After Roper et al. 1995.)

different design and species (aversive conditioning in laboratory rabbits), Wagner et al. (1973) showed that surprising episodes *after* conditioning trials interfere with learning. Together, these results suggest that surprise does not enhance learning simply by heightening physiological responses, nor do surprising events cause reduced learning due to interference. Instead, a surprising event may draw resources from other cognitive processes.

Animals may also direct working memory resources away from a stimulus. In an experiment that combined a delayed matching-to-sample and a delayed symbolic matching-to-sample procedure, pigeons learned to forget a previously presented sample (fig. 4.5). This procedure presented a pigeon with a red or green sample followed by a white or blue "remember cue." After the remember cue, the subject matched the red or green sample in an ordinary delayed matching-to-sample task. If an open or solid dot (the "forget cue") followed the red or green sample, the experiment tested the pigeon in a symbolic matching-to-sample task using the dot as the sample stimulus and horizontal and vertical lines as the comparison stimuli. Thus, the open or solid dot meant that the pigeon should "forget" the first sample. Periodic probe trials presented "forget cues" followed by red and green comparison stimuli. This manipulation caused a significant decrement in performance on the probes compared with the delayed matching-to-sample tasks, consistent with directed forgetting (Roper et al. 1995).

Maintaining Reference Memory

A foraging jay retrieves information about prey types and locations from reference memory when it returns to foraging after engaging in some other

activity. We can compare reference memory to the storage of books in a library. A forager must organize and index memories effectively or they will be lost. Surprisingly, forgetting does not typically erase long-term memories; it just makes them difficult to find. The contextual attributes of a memory at encoding provide the cues needed to locate information from reference memory at retrieval. Memory researchers call this phenomenon *encoding specificity*.

If, for example, a jay learns a new prey type while it is ill or agitated, it will theoretically be better able to retrieve this information when it is again ill or agitated. Memory researchers call this type of encoding specificity *state-dependent memory*. Duplicating external attributes of the learning context (such as being in a meadow or a rainstorm) can reactivate and improve recall. Substantial differences between two learning contexts reduce confusion at recall. Similarly, subjects have better recall when many attributes of the learning context are present because each attribute can potentially reactivate the association (reviewed in Roberts 1998).

Synopsis

A forager can learn what to eat and what to avoid through classical conditioning. As studies of taste aversion show, the biological relevance of the stimuli constrains and facilitates this learning. Learned associations are stored and retrieved in a dynamic and multifaceted memory. Memory retrieval is influenced by events that happen before or after encoding, as in interference. Animals can optimize short-term working memory through rehearsal and directed forgetting, while contextual cues and chunking facilitate retrieval. Learning and memory allow a forager to exploit new biologically relevant patterns in its environment and to recall such information to increase its foraging success.

4.5 Locating Food

A foraging blue jay will have trouble returning to a prime food patch unless it remembers where the patch was and how to get there. Researchers study how foragers orient in space, define locations, and remember locations under the rubric of *spatial cognition*. Because all mobile animals must navigate space, spatial cognition is a central subject in comparative cognitive research. *Scatter-hoarding* species (which make a single deposit to each of many cache sites) represent an extreme case of reliance on spatial cognition: they rely heavily on spatial memory to retrieve their caches. Social animals may exploit a conspecific's spatial knowledge through *social learning* of food locations.

Spatial Orientation

Our hypothetical jay perches on a branch and tries to recall the location of a food cache. It has many cues to the cache location: the sun, distant mountains, the distant odor of the ocean, nearby trees, branches, and leaves. We can divide these external cues into two classes: positional and directional. Positional cues are usually landmarks close to the goal (i.e., *local*), and directional cues are usually distant landmarks, but could also be gradients of concentration, intensity, or size (Jacobs and Schenk 2003). Directional cues provide compasslike information: direction, not distance. Distant landmarks that serve as directional cues are termed *compass marks* (Leonard and McNaughton 1990). A *beacon* is a landmark that coincides with the goal. The forager can, therefore, choose from several *frames of reference*. It can simply approach the beacon, it can triangulate within an array of positional cues, or it can move in the direction of a compass mark or along a gradient.

An object's position within an array of positional cues is its *relative position*, while its position relative to directional cues is its *global* or *absolute position* (Brodbeck 1994). Both positions are relative to some subset of terrestrial cues, but the distinction between them reflects real phenomena. We see the dissociation between relative and absolute frames of reference in rodents and birds, both in the laboratory (Brodbeck 1994) and in the field (Healy and Hurly 1998; Jacobs and Shiflett 1999). For example, rufous hummingbirds searched for an artificial flower in its absolute position if its neighbors were greater than 80 cm apart, but searched at a position relative to an array if the flowers were 10 cm apart (Healy and Hurly 1998).

In many mammalian species, females and males prefer different frames of reference. In several polygamous species, females prefer local cues while males prefer distant or directional cues (reviewed in Jacobs and Schenk 2003). Sexual selection seems to favor this sex difference because males must track the spatial distribution of females (Gaulin and FitzGerald 1989). Tracking females requires long-distance navigation in unfamiliar territory, which cannot rely on familiar local cues.

Gradients

Any forager, regardless of brain size, can orient to a gradient, as in the case of phototaxis. Animals find many gradients in nature, such as polarized light, chemical plumes, and temperature or elevation gradients (Dusenbery 1992). A literal compass is a tool for orientation in a gradient of magnetic polarity (both invertebrate and vertebrate foragers use magnetic polarity to orient; Goodenough et al. 2001). Foragers can use gradients to orient in a one-dimensional map produced by linear changes in a single variable (e.g., temperature or concentration). These maps have the advantage of perceptual simplicity and also allow for extrapolation. A forager following a regular gradient can keep track of its movements, but it can also weather disruptions in continuity by calculating the expected concentration, elevation, or intensity after moving a known distance. This one-dimensional map forms the basis for all spatial orientation and may be necessary for large-scale movements, such as migration (Wiltschko and Wiltschko 1996). Extrapolation to unknown terrain represents the key advantage of this type of orientation, although noise in the signal and the forager's ability to perceive fine gradations limit its accuracy. Animals can, therefore, create only low-resolution maps using gradients (Jacobs and Schenk 2003; Wallraff 1996).

Landmarks

A more complex orienting method requires the ability to perceive and recognize unique objects, such as certain rocks, trees, or mountains. Use of landmarks lets a forager orient within small local arrays of objects. Different species use landmarks in different ways. Some animals encode a "snapshot" of the goal and associated landmarks. Researchers have studied this process in honeybees (Dyer 1996). The foraging bee encodes an image on her retina at the food source. When she returns, she moves such that the incoming visual image matches the stored retinal image. This simple algorithm, *template matching*, returns her accurately to the flower's location. She also uses the earth's magnetic field to encode compass direction. If she learns a retinal image from the south of a flower, for example, when she returns to that flower, she again approaches it from the south to rematch the image (Collett 1996).

We see more complex landmark use in birds and mammals. These foragers can recognize unique features of a specific landmark in three dimensions. In these cases, the forager remembers unique features of the landmarks themselves and the spatial associations among them. With this information, the forager can triangulate to relocate its goal relative to the landmarks. This process, described by different theoretical models (e.g., vector sum model; Cheng 1994), does not require any notion of absolute direction.

These two examples illustrate an important point: different cognitive mechanisms can accomplish the same result. Since the overt behavior is the same (accurate reorientation to a remembered location), we can discover such differences only through experimental manipulation. Collett and colleagues demonstrated such a difference in two classic experiments on spatial memory in honeybees and female Mongolian gerbils (Collett 1996; Collett et al. 1986). Both species accurately recalled a single location that was between two vertical columns. When the experimenters increased the distance between the columns during the forager's absence, the bee and the gerbil responded differently.

The bee matched her retinal image and hence increased her distance from the columns such that their retinal distance from each other matched her stored image. The gerbil, using her mammalian depth perception, searched the correct distance and angle from each of the two columns. Although the gerbil may have encoded more information about the landmarks, the honeybee's simpler solution works just as well under normal foraging circumstances.

Cognitive Maps

Spatial cognition researchers view the cognitive map as the most sophisticated method of spatial orientation. Edward Tolman first proposed that simple stimulus-response mechanisms could not explain the behavior of rats in a maze. He suggested instead that rats store a representation of the maze, a *cognitive map*, independent of immediate contingencies (Tolman 1948). An animal with a cognitive map can demonstrate its capacity by taking novel routes across unknown terrain. For this behavior to be convincing evidence that the animal is following a mental representation of the new route, the animal must create the route without intermediary landmarks or beacons. For example, a squirrel travels 200 meters east to a new foraging area. It then returns to that area using various methods, such as orienting to known landmarks (e.g., arrays of known trees). Later, the squirrel travels 200 meters south to a second novel foraging location. If the squirrel has created a cognitive map, it can then calculate the direction and distance of a vector linking the eastern and southern foraging sites. A squirrel with a cognitive map can navigate between the two sites even without a beacon at the eastern site (e.g., a tall tree, the sound of a waterfall) or a chain of familiar landmarks. The squirrel can recall the cognitive map as often as necessary to create new detours and shortcuts.

Recently, Jacobs and Schenk (2003) proposed a new theory to explain the cognitive map, drawing on Gustav Kramer's map-and-compass hypothesis (Wallraff 1996). Here the cognitive map is composed of two submaps: the *bearing map* (derived from directional cues) and the *sketch map* (derived from positional cues). Two independent neural circuits within the hippocampus subserve these maps. This *parallel map theory* proposes that animals need both hippocampal subfields to create a cognitive map. This may be why cognitive maps are limited to birds and mammals, since other vertebrates have only one subfield enlarged (Jacobs and Schenk 2003). To date, the best evidence indicates that the honeybee does not form a cognitive map (Dyer 1996), but similar experiments have not been conducted using other invertebrates, such as predatory cephalopods, stomatopods, or spiders, which may have greater need for a cognitive map.

Spatial Cognition in Food Hoarders

By storing food and remembering the locations, a forager can even out a food distribution that is clumped in time or space and protect it from competitors. Scatter hoarders use many locations and face special memory demands because they must maintain a large quantity of information over long periods. Scatter hoarding has been found only in birds and mammals (Vander Wall 1990). The study of food-hoarding behavior and how it is related to cognitive specialization is still a new field and has attracted both support and controversy, which has led to several recent reviews of this literature (Hampton et al. 2002; Macphail and Bolhuis 2001; Shettleworth 2003). In general, studies of cognitive specialization in food hoarders have asked how and why such species differ in the ways in which they remember spatial locations and how food hoarding is related to separable, specialized cognitive abilities.

Cue Use and Frames of Reference

The need to encode and forget temporary cache sites may have led to specialization in encoding. Food hoarders might encode spatial information differently from other information, and from nonhoarders, increasing capacity by efficiency. For example, if food hoarders encoded cache sites as unique places on a global map defined by large, distant landmarks (absolute location), this would have several advantages. First, such landmarks are likely to be stable (Biegler and Morris 1993). Second, each site would have unique coordinates, regardless of how similar the closer landmarks (e.g., local vegetation) were between cache sites. Third, unique sites should reduce interference during encoding: the more uniquely a cache is encoded, the less interference among caches. Moreover, if the cache can be encoded not only in terms of a unique place, but also by other characteristics, such as the time of caching or the contents of the cache, all of these features would improve accuracy, based on what we know about memory in general.

When experimenters moved a feeder with a distinctive color and pattern that had been previously baited, scatter-hoarding chickadees searched first at its previous location in the room (absolute location), then at its previous position within an array of feeders (relative location), and finally, after finding no bait, at the feeder that had the correct color and pattern. Nonhoarding juncos, in contrast, searched equally at all locations, suggesting no preference for any available frame of reference (Brodbeck 1994). Clayton and Krebs (1994) found similar results when they compared hoarding and nonhoarding corvids. In the field, free-ranging fox squirrels also preferred to orient first to the absolute location of their goal (Jacobs and Shiflett 1999).

Another method scatter hoarders may use to reduce inference among caches is to distinguish between them by their contents. Sherry (1984) found that black-capped chickadees retrieved preferred seed caches first, suggesting that they chunk items in their memories just as rats chunk baits by type in radial-arm maze studies.

Spatial Memory

Because species vary widely in their reliance on cached food, investigators have devised spatial tasks to examine species and population differences that may correlate with hoarding behavior. For example, within corvids, Clark's nutcrackers rely most heavily on caches, and pinyon jays slightly less. Mexican jays may rely on some caching, but scrub jays do not rely heavily on cached food for survival. The degree of cache reliance paralleled laboratory cache retrieval performance: Clark's nutcrackers outperformed pinyon jays, which in turn outperformed scrub jays (Balda and Kamil 1989). Clark's nutcrackers and pinyon jays also performed more accurately than did Mexican and scrub jays on a radial-arm maze analogue (Kamil et al. 1994). Corvid performance on a *spatial* delayed non-matching-to-sample task was also correlated with reliance on stored food (Olson et al. 1995). Clark's nutcrackers tolerated the longest delay between sample and choice, compared with pinyon, Mexican, and scrub jays. However, when experimenters tested memory for color rather than location, they found a different pattern: pinyon and Mexican jays tolerated a longer delay than nutcrackers or scrub jays. Under certain conditions, Clark's nutcrackers can show accurate cache retrieval over 270 days after caching (Balda and Kamil 1992). In a later study, nutcrackers and pinyon jays once again outperformed Mexican and scrub jays at retrieval intervals up to 60 days (Bednekoff et al. 1997).

The same result was obtained in a working memory task in parids. Biegler et al. (2001) compared the accuracy, capacity, and resolution of spatial memory in coal and great tits using delayed matching-to-sample techniques. Performance decreased for both species with increases in the number of sample locations to be remembered, the delay length, and spatial clumping of the choice objects. Again, the food-hoarding coal tits outperformed the nonhoarding great tits in the delay length they could tolerate—that is, in the persistence of spatial memory.

Scatter hoarding is also found in many mammals, particularly granivores and carnivores (Vander Wall 1990), and similar memory results have been obtained in granivores such as desert rodents and tree squirrels (Jacobs 1995). Scatter-hoarding kangaroo rats are more accurate at cache retrieval than larder-hoarding pocket mice (Rebar 1995). In addition, kangaroo rats can accurately retrieve caches in open spaces without landmarks after a 24-hour delay. With landmarks, kangaroo rat performance did not change even after a 10-day delay (Barkley and Jacobs 1998).

Such persistent spatial memory might increase proactive interference and degrade performance in some cases. In a simple task in which the correct response varied among a few spatial locations, scatter-hoarding chickadees indeed suffered more interference than nonhoarding juncos (Hampton et al. 1998).

Memory of Caching Events

Perhaps the most advanced organization of spatial memory includes not only a food item's location and contents, but also memory for the unique foraging episode when the item was cached. Recent studies have demonstrated memory for events, or episodic-like memory, previously described only in humans, in the scatter-hoarding scrub jay. In these studies, scrub jays learned either that worms spoiled after long storage (5 days) or that they did not. After a long delay between caching and retrieval, the group that had learned that worms spoil searched first for nonperishable peanuts, despite their normal preference for worms. The group without any experience of spoilage expressed their unaltered preference and searched for worms first and peanuts second (Clayton and Dickinson 1998, 1999). Many questions remain about nonhuman episodic memory, yet this experiment demonstrated that a foraging jay could encode a specific event in time and could use this data to optimize subsequent foraging decisions.

Social Learning

Social foragers may initially learn where to find food from other foragers. Social learning can range from guppies locating food by swimming with more knowledgeable conspecifics (Swaney et al. 2001) to the exceptional honeybee dance language (see Shettleworth 1998 for review; Riley et al. 2005 for recent research). Multiple causes can underlie social learning, or the appearance of social learning, so mechanisms must be carefully investigated (see discussions in Galef 2004 and Heyes and Galef 1996). *Local enhancement* (or *stimulus enhancement*) does not require direct contact between individuals. One individual's activity or its effects simply attract the attention of another individual, which then learns on its own. Similarly, in *social facilitation*, the presence of conspecifics may affect the motivation or arousal of the observer and allow it to learn independently. *Imitation* and *emulation*, which we will discuss later, are more complex forms of social learning.

Two recent studies with corvids illustrate *observational learning* of foraging locations. One study showed that free-living Florida scrub jays were able to learn a novel food patch by watching a trained demonstrator forage in the center of a moving ring (Midford et al. 2000). Another found that ravens not only could learn the location of food by observing conspecifics caching, but also cached behind occluders to prevent such observation (Bugnyar and Kotrschal 2002).

Communication is a special type of social learning. The honeybee dance language is one of the best-studied and most sophisticated methods of communicating food location in the animal kingdom. In addition, several social species call in the presence of food, including primates, dolphins, bats, and many species of birds (reviewed in Gros-Louis 2004). Recent evidence suggests that food calls, along with many alarm calls, may be "functionally referential"; that is, the call is given reliably in the presence of the referent, and the receiver of the call behaves consistently whether or not it can detect the referent. Functional referentiality is usually tested using playback experiments. Domestic chickens and tufted capuchin monkeys have both demonstrated responses particular to food calls in playback experiments, indicating that these calls direct individuals specifically to food (reviewed in Gros-Louis 2004).

Synopsis

Foragers rely on a variety of cognitive abilities to locate or store food items. From the simplest phototaxis to a cognitive map, mobile foragers need some form of spatial cognition. Foragers use external cues, such as beacons, gradients, and arrays of landmarks, to orient and to memorize the location of food sources. Different species, and even males and females of a single species, may use different frames of reference for their spatial orientation. Scatter-hoarding species face the additional problem of creating and relocating hundreds or thousands of cache sites, which could explain observed species differences in performance on abstract and naturalistic tasks measuring spatial memory. Social learning can also help a forager locate food by observation or communication.

4.6 Techniques for Obtaining Food

The omnivorous blue jay faces a final cognitive challenge: it must learn to extract food from the environment. It may need to do anything from prying up bark to capture insects underneath to opening a discarded berry container. The jay must learn those food-handling techniques that are not innate.

Instrumental Conditioning

Instrumental or operant conditioning refers to a situation in which an animal learns that its own behavior, in the presence of certain stimuli, is instrumental in causing a particular outcome. The study of instrumental conditioning began with the work of E. L. Thorndike (1874–1949), who conducted the first controlled studies of learning in the laboratory (Thorndike 1911). To compare the "intelligence" of species directly, he developed cages known as *puzzle boxes*, in which a hungry animal had to trigger a release mechanism from inside the box to reach food outside. When first placed in a puzzle box, an animal moved randomly until it accidentally triggered the escape mechanism. In subsequent trials, the animal tended to repeat the behaviors that had occurred just before its escape, whether or not those behaviors opened the apparatus. This process of repeating the behaviors that preceded success produced a gradual, negatively accelerated *learning curve* (as discussed under "conditioning mechanisms" in section 4.4) when Thorndike plotted time to escape against trial number. From this observation, Thorndike formulated the *law of effect*: in a particular context, behavior that is followed by a satisfying event strengthens the association between the context and the behavior, causing the behavior to become more likely should the context recur. This law formed the basis for instrumental learning theory.

Behavioral psychologists use two types of procedures to study instrumental conditioning: discrete-trial and free-operant procedures. In discrete-trial procedures, the subject makes the instrumental response once per trial, such as triggering the escape mechanism of a puzzle box. Likewise, an experiment may require that a rat turn left in a maze to obtain a reward. After the response, the investigator removes the subject from the apparatus. In free-operant procedures, the subject repeats its response freely. The operant chamber is the original and most typical free-operant apparatus and has proved to be a critical tool in the study of instrumental conditioning due to the ease of collecting data.

Both types of procedures rely on the pairing of a behavior with a reinforcing outcome, or *reinforcer*, such as food. One can deliver the reinforcer every time the subject makes the required response (*continuous reinforcement*) or only every so often (*partial reinforcement*). Behavioral psychologists use four basic schedules of partial reinforcement. In an *interval schedule* the subject earns reinforcers for responses after a given time interval. In a *ratio schedule* the subject earns reinforcers after a specified number of responses, such as lever presses or key pecks. The time and number requirements can be fixed (staying the same from trial to trial) or variable (changing from one trial to next), giving four possibilities: variable interval, variable ratio, fixed interval, and fixed ratio schedules. The reinforcement schedule influences the behavior of a subject in predictable ways; for example, subjects in fixed interval schedules begin to respond just before the end of the fixed interval (Roberts and Church 1978; see Domjan 1998 for thorough discussion of instrumental conditioning).

Biology constrains instrumental conditioning, just as it does classical conditioning. Foragers do not have to learn all the behaviors associated with feeding; the corollary of this statement, that some behaviors cannot be unlearned, is *instinctive drift*.

Breland and Breland (1961) first demonstrated instinctive drift in their instrumental conditioning of animals for commercial advertising. For example, they would train a raccoon to drop a coin into a box using the *method of successive approximations*, in which they rewarded the animal for behaviors progressively closer to the desired one. However, the raccoon's behavior proved less malleable than predicted. It would rub the single coin, or later two coins, together, thereby delaying reinforcement. Despite the obvious cost in reinforcements, the raccoon could not suppress its innate foraging movements of rubbing small objects together. These findings have inspired a movement toward a functional perspective in learning theory that emphasizes biological relevance (Domjan 2005).

Imitation

A jay may learn foraging techniques by imitating a conspecific's successful technique. However, as mentioned above, researchers must carefully identify the processes involved. In one famous example, a wild population of English blue tits learned to open milk bottles and drink the cream (reviewed in Shettleworth 1998). Debate ensued over how this skill spread through the population. Sherry and Galef (1990) showed experimentally that the spread of this skill did not require imitation, but could have been accomplished by local enhancement and social facilitation.

Imitation can also be confused with *emulation*. Whereas when an individual imitates, it copies the action of a model, when an individual emulates, it learns that the environment can be manipulated to achieve a particular goal. For instance, an emulator might see a model open a hinge by poking out a pin and learn only that the pin comes out. During replication, an imitator would poke the pin out, whereas an emulator might pull it. Emulation is arguably as cognitively complex as imitation, but may require different mechanisms. The mechanisms involved in both processes are still highly controversial (see reviews in Caldwell and Whiten 2002; Zentall 2004).

In the most definitive test for imitation, the *two-action test*, models demonstrate different solutions to the same problem to different experimental groups. If the subjects use the method they observed, this indicates imitation rather than emulation. For example, demonstrator Japanese quail depressed a treadle with the foot or the beak while one experimental group watched each technique. When tested, the quail generally used the technique they had witnessed. In a further demonstration, observers were more likely to imitate a demonstrator that received food rewards for its actions than one that did not, suggesting that the imitator may also represent the action's purpose—in this case, obtaining food (reviewed in Zentall 2004).

A recent study distinguished between *action* imitation and *cognitive* imitation (Subiaul et al. 2004). In a typical serial learning task, demonstrator rhesus monkeys were taught series of photographs. The monkeys were required to press each photograph on the screen in order, although the location of the photographs was changed in each screen. The observer monkeys were able to gain some information about ordinal position by watching the demonstrators that raised their performance significantly above baseline. This effect was not the result of social facilitation or emulation based on the feedback given by the computer. Therefore, under some circumstances, animals may learn rule-like information from observing conspecifics.

In other cases, animals may learn *not* to imitate one another. Pigeons in a situation in which the actions of a skill demonstrator deliver food to the observer regardless of the observer's behavior do not learn the skill. In contrast, with a small change in the apparatus, the observer is not rewarded during the experience, and under these conditions, observers readily learn to copy the movements of the demonstrator (Giraldeau and Lefebvre 1987). This observation suggests that learning of a particular food-handling technique may depend on whether the subject stands to gain from learning that skill.

Teaching

If animals can learn from others, it stands to reason that behaviors that promote such learning experiences could also evolve. Caro and Hauser (1992) defined teaching functionally as a change in behavior in the presence of a naive individual that is not immediately beneficial to the teacher and helps the naive individual learn. Common chimpanzees may teach their young how to use stone hammers and anvils to open coula nuts (Boesch 1991). Mother chimpanzees in Tai National Park behaved in ways that could facilitate learning, including leaving hammers near anvils when offspring were present, although they usually carried the hammers away (the hammers were used by offspring on 46.2% of 387 such occasions), or bringing nuts or hammers to a young chimpanzee at an anvil (588 occasions, leading to a 20% increase in nuts eaten per minute by offspring). On two occasions, mothers adjusted the orientation of the hammer or the nut, seemingly correcting the infant's use of the technique.

Teaching may be prevalent in species with elaborate predatory behavior, such as birds of prey and carnivores. Among these species, ospreys, domestic cats, and cheetahs demonstrably increase the foraging effort they require from their offspring, from bringing them dead prey to live but wounded prey and finally live prey that are allowed to escape for recapture (reviewed in Caro and Hauser 1992). Some spiders may behave similarly (Wilson 1971). In most of these species, it remains to be demonstrated that this behavior actually facilitates learning. However, a laboratory study with domestic cats found that kittens whose mothers were present and interactive during exposures to live prey learned hunting skills earlier than control kittens whose mothers were not present (reviewed in Caro and Hauser 1992).

As with imitation, cognition researchers want to understand the cognitive processes underlying teaching. It might seem that teachers require a *theory of mind* (a representation another's mental states) to be sensitive to the needs of the pupil. Caro and Hauser maintain that although such a representation would "almost certainly enhance the utility of teaching" and may be present in some species, it is not necessary. To be useful, the teacher must have a mechanism for discriminating which individuals lack skills or knowledge. Distinguishing the actual mechanisms involved will require experimental manipulations. As with other behaviors we have discussed, species differences in the cognitive basis of teaching are likely to emerge.

Insight

Can an animal use existing knowledge to produce a novel foraging technique? One way of doing so might be through *insight*, a novel viewpoint on a situation that can enable undetected relationships to suddenly become apparent. Animals must solve problems without overt trial-and-error learning, innate programmed responses, or observation before insight can be considered. Early experiments by Kohler (1925) are frequently cited as the seminal research on insight in human and nonhuman psychology (reviewed in Ormerod et al. 2002). Working with a group of captive chimpanzees, in one experiment Kohler (1925) hung bananas from a high place and gave the chimpanzees a box. The chimpanzees solved this problem by moving the box so that stepping on it allowed them to reach the bananas. Later they were also able to stack several boxes to solve a similar problem (fig. 4.6). Success tended to come suddenly after a period of no progress, not gradually after many approximations, suggesting insight.

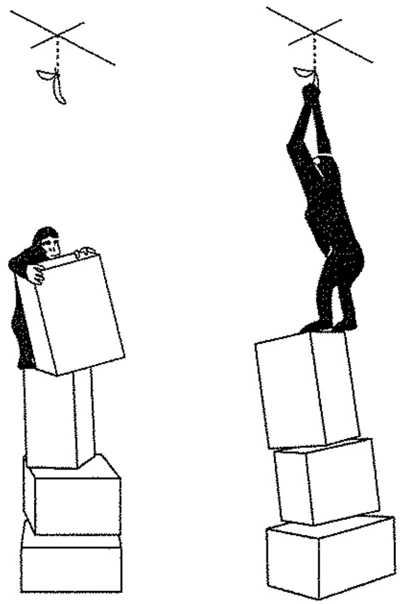


Figure 4.6. Testing for insight in chimpanzees. Captive chimpanzees trying to reach a hanging banana appear to suddenly realize a solution to the problem, suggesting insight. In the drawing at the right, a chimpanzee has stacked three boxes to reach the bananas overhead. In the drawing at the left, another is in the process of stacking four boxes to reach the goal. (After photographs in Kohler 1925.)

Although Kohler's chimpanzees had no previous experience with the exact problem presented to them, an experiment by Epstein et al. (1984) cast doubt on Kohler's results. Pigeons trained separately to push a box toward a randomly placed target and to stand on a box to peck a fake banana put these behaviors together to solve the equivalent problem, reportedly through stimulus-response chaining rather than insight. Pigeons trained to perform only one of the subtasks (e.g., climbing but not pushing) failed to reach the banana. However, why the pigeons pushed the box specifically toward the banana was unclear.

A study of hand-reared ravens controlled more precisely for previous experience (Heinrich 1995). The ravens faced the following problem: how to retrieve food attached to a branch by a long string. A raven had to land on the branch and use its beak and foot to pull up the string in stages. Once the raven obtained the food, it had to suppress its natural tendency to fly away because the food was still connected by the string. Despite the complexity of the motor sequence involved, several ravens performed this task correctly without apparent trial-and-error learning. Although pulling and stepping may be an innate motor pattern in birds (see review in Thorpe 1963), several ravens never completed the task, and the ones that did showed a prolonged delay. Heinrich argued that assembly of the steps into a coherent, novel action, not the origin of the individual steps, is crucial for demonstrating insight. These studies suggest that under appropriate circumstances, animals may create novel foraging techniques without trial and error.

Tool Use

Techniques for obtaining food may include the use of tools. Many animals have been observed using tools, including insects, crabs, rodents, elephants, and many primates (reviewed in Griffin 2001). A *tool* is a material object that an animal manipulates as an extension of its body to achieve an immediate goal. Sea otters, for example, use a rock to crack a prey item's shell; Egyptian vultures and chimpanzees use rocks in a similar way. Many other taxa use a thin stick to extract insects or other food items from crevices; examples include the Darwin's woodpecker finch, common chimpanzee, and New Caledonian crow. Tool use may be acquired by the processes described previously or may be innate. Cognition researchers are particularly interested in whether the tool-using animal understands the relationship between the tool and its use (the *means-ends* or *cause-effect* relationship).

Hauser (1997) demonstrated that cotton-top tamarins can discriminate the functional properties of a tool. Hauser gave tamarins a choice between a functionally intact tool and one that he had modified to make it nonfunctional. For example, the tool might be a cane placed with a piece of candy inside its hook so that the monkey could use it to pull the candy in. A nonfunctional option might be the cane with the candy outside of its hook. In a series of experiments, tamarins chose the functionally intact tool more frequently.

However, capuchin monkeys can successfully use tools without understanding the means-ends relationship. Visalberghi and colleagues (Visalberghi and Limongelli 1996) tested capuchins and chimpanzees using a clear plastic tube with a cuplike depression in the middle, known as the "trap tube" (fig. 4.7), and a reward placed outside the trap at one end of the tube. To extract the food, the animal had to push a stick through the tube, pushing the food out of the tube while avoiding the trap. Previously, three of four monkeys had used sticks to obtain rewards from tubes without traps (Visalberghi and Trinca 1989). With the trap, however, the monkeys needed to push from the correct end. When tested with the trap, three of four monkeys could not extract food more than half the time, even after 140 trials. The fourth monkey learned the task after 90 trials, but apparently learned by rote. She continued to push from the side farthest from the food (as the trap requires), even when the investigators rotated the trap upward (and it no longer acted as a trap). Chimpanzees showed more signs of means-ends understanding in performing this task. Of five, two solved the original trap tube and transferred this skill to a variant in a way that suggested they understood the intermediate goal of avoiding the trap.

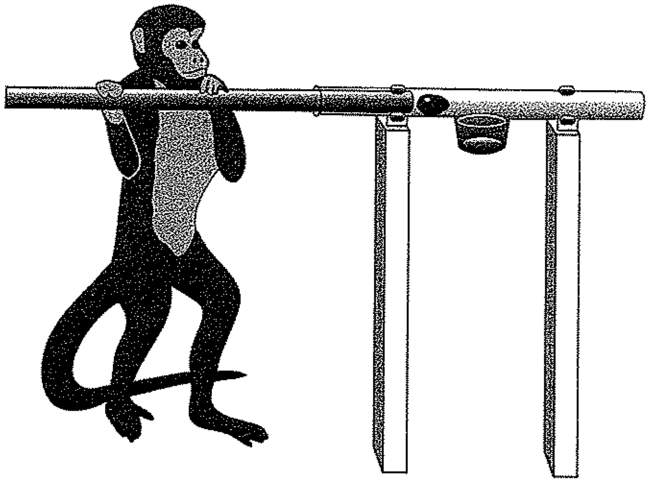


Figure 4.7. Testing for means-ends understanding with the trap tube. In this experiment, the subject must use a stick to push a reward out of the tube. If the subject pushes from the wrong direction, the reward will fall into the trap. Here, a capuchin monkey is about to push the reward into the trap. (After a drawing in Shettleworth 1998 of a photograph in Visalberghi and Limongelli 1994.)

Modification of tools for a particular task also suggests understanding of the means-ends relationship. New Caledonian crows modify their tools into two different shapes (a hook or a jagged tool) as appropriate for removal of insects from different holes, and they shorten the length of a tool when necessary (Hunt 1996). Recent studies have shown that these crows can choose the right length of stick without trial and error (Chappell and Kacelnik 2002), and one individual bent a piece of wire into an appropriate tool (Weir et al. 2002).

Synopsis

Animals can use different cognitive skills to acquire foraging techniques. A forager may learn techniques by trial and error through instrumental conditioning, but within the constraints of innate biases. Imitation may be an efficient way to learn a successful technique from a conspecific. Teaching may also play a role in transferring foraging techniques. Sometimes animals may use insight to produce a correct technique the first time they encounter a problem. Many animals use tools to forage, though they may not always understand why the tool works. The cognitive mechanisms underlying many of these behaviors are still being investigated.

4.7 Summary

Foraging requires a broad range of cognitive skills. Foragers must perceive the environment, learn and remember food types, locate food resources, and learn techniques for extracting food items once found. Students of foraging need an understanding of these processes because they enable and constrain foraging behavior. Theorists can use data on animal cognition to develop more realistic foraging models. Foraging researchers can also pursue cognitive questions that provide potentially relevant information about foraging decisions. The separate traditions of psychology and behavioral ecology have formed a barrier to this interdisciplinary research. Psychologists have focused on process (learning, memory, and so on) using a limited number of species in highly controlled situations (Beach 1950), while behavioral ecologists have focused on functional categories of behavior (foraging, reproduction, etc.) using many species. Investigators are now working to break down these barriers, and foraging is a key point of contact between behavioral ecology and animal psychology. We hope that this chapter will help inspire future interdisciplinary research efforts. New data could bring answers regarding the survival value of cognition and the mechanisms of foraging within our grasp.

4.8 Suggested Readings

There are a number of comprehensive textbooks on animal cognition. *Cognition, Evolution and Behavior* (Shettleworth 1998) provides significant detail suitable for upper-division or graduate students. *Principles of Animal Cognition* (Roberts 1998) offers the most comprehensive discussion of animal memory. Another good introductory text is *Animal Cognition: The Mental Lives of Animals* (Wynne 2001). Conditioning is thoroughly covered in *The Principles of Learning and Behavior* (Domjan 1998), while *Animal Minds: Beyond Cognition to Consciousness* (Griffin 2001) represents the field of cognitive ethology. For a broad sampling of animal cognition, *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition* (Bekoff et al. 2002) and *Comparative Cognition: Experimental Explorations of Animal Intelligence* (Zentall and Wasserman 2006) are good choices. For in-depth coverage of specific topics, the Comparative Cognition Society (www.comparativecognition.org) publishes free-access online textbooks on animal cognition, including *Avian Visual Cognition* and *Spatial Cognition*.

Part II

Processing, Herbivory, and Storage