

animal Behavior

How and Why
Animals Do the
Things They Do



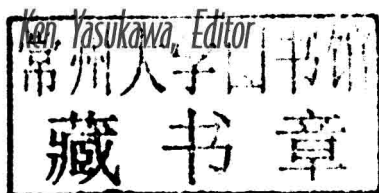
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Ken Yasukawa, Editor

Animal Behavior

How and Why Animals Do the Things They Do

Volume 2: Function and Evolution



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Finding Food: Foraging Affects All Aspects of an Animal's Life

Anna Dornhaus

INTRODUCTION

Why do horses sleep only 3 hours a day, while lions may sleep 18 hours? Why do birds commonly sing at dawn rather than in the afternoon? Why are chimpanzees violent and patriarchal in their social life, while the closely related bonobos are peaceful and females dominate males? *Behavioral ecology* is the science that seeks to explain the diversity in lifestyle we find in animals, including the origins of our own human habits. Foraging plays a central role in this: all of the above questions have been answered by referring to the foraging needs of these respective species, demonstrating the central role that finding food plays in the evolution of animal behavior.

Foraging in animal behavior research refers to finding and collecting resources. Foraging for most animals is one of the most energetically costly and risky activities, particularly if the animal has to leave its home or shelter and cover great distances. Because of this, the requirements of foraging affect many other aspects of an animal's life. For example, plant matter has a much lower energy density than meat, which means that herbivores, such as horses (*Equus ferus*), may need to spend a lot more time collecting food than carnivores such as lions (*Panthera leo*), who can afford to spend a lot of time resting (Lesku et al., 2009). Some animals have so little reserves that they have to ration energetically expensive activities depending on the amount of food

found each day—this is thought to be the case for small birds in cold climates, who can only afford to sing (to defend territory or attract mates) when they have survived the night and find that they still have fuel left over, leading to a dawn chorus (Hutchinson et al., 1993; Thomas, 1999). In the longer term, adaptations to the necessities of foraging change a species' overall life style. For example, bonobos (*Pan paniscus*) eat leaves and shoots of plants, which are common and easy to find. This allows groups of related females to stay together, which led to the evolution of strong female-female bonds. Chimpanzees (*Pan troglodytes*), on the other hand, mostly eat fruits and other foods that are patchy in distribution and require travel—which disadvantages females with infants, who travel slowly and thus have to search on their own if they want to avoid arriving at a resource already depleted by others in the group. This may prevent intense bonding and thus lead to the more patriarchal, aggressive societies we see in chimpanzees compared to bonobos (Wrangham, 1993). Even our unique human traits, such as large brains, cooperation, and trading, are thought to depend in large part on novel foraging behaviors by early hominids (Pennisi, 1999; Boehm, 2004).

Foraging is among the best-studied animal behaviors, due to the fact that foraging animals typically have to leave their shelter and move around, making them more visible and susceptible not only to predation but also to research (Kamil and Roitblat, 1985). The second advantage of foraging behavior, from a research perspective, is that success or failure in foraging is more easily defined and measured than in many other activities: a foraging animal collects a food of a certain caloric value in a certain amount of time. This led to foraging behavior being one of the first topics in which quantitative and predictive models were used intensively. The field of modeling foraging behavior came to be known as *optimal foraging* (Pyke et al., 1977; Stephens et al., 2007). The fact that measuring foraging success seemed so straightforward allowed models to actually predict optimal behavioral strategies in extraordinary detail. This led to some criticism, as some felt that such precise predictions were unrealistic or unhelpful (reviewed in Stearns & Schmid-Hempel, 1987; Raine et al., 2006). However, all fields of studying animal behavior, and perhaps of organismal biology, have benefited from the idea that the "target" of selection, or the optimal behavior, is not necessarily obvious to a casual observer and can be derived quantitatively and objectively within given constraints. Much of biology is now emulating similar approaches, trying to clarify precisely which factors will drive evolution of organismal traits and in what directions. These can be nonintuitive, particularly in cases where subtle differences in assumptions can actually lead to differences in the direction of selection (Kacelnik, 1993).

One behavior thus studied is the phenomenon of “partial loads” in *central-place foragers*, particularly bees (Raine et al., 2006). Honey bees visiting a plentiful nectar source will often not carry as much back to their hive as they could, despite the fact that the same forager will make multiple subsequent trips to the same source to collect more nectar. This seems counterintuitive and indeed inefficient: *why not carry a full crop with every trip?* Mathematical models have helped us to understand the conditions under which partial, instead of full, loads may be advantageous to bees. First, if a flower offers nectar at decreasing returns, that is, the last bit of nectar is harder to extract, then it may be worth leaving before a full load has been collected in order to visit more other sources (Charnov, 1976). Second, it may be that if heavy loads impose high transport costs, and if a bee's lifespan is affected by how hard it has to work, the total nectar collected in the life of a foraging bee is in fact higher if only partial loads are collected (Schmid-Hempel et al., 1985; Wolf & Schmid-Hempel, 1989). Third, bees can recruit their nestmates to a rich food source; it may be worth limiting the amount of time the first forager spends there in favor of recruiting more bees to the resource before it is discovered by competitors, thus increasing the success of the group as a whole at the expense of the success of that first individual (Núñez, 1982; Varju & Núñez, 1991). Finally, since information about new, superior sources could arrive at any time at the hive, a forager may prefer to return to the hive frequently to check for such information in order to prevent wasting time at an inferior resource (Dornhaus et al., 2006). Mathematical models have allowed researchers to derive clear, quantitative predictions not only about how early a forager should leave a resource but also about which factors should affect this decision and how—for example, according to the third hypothesis, bees should collect smaller loads if the resource is of high quality, whereas the fourth hypothesis predicts that they should collect larger loads in this case. Empirical tests have revealed that the former is the case, supporting the idea that honey bee foragers sacrifice their own foraging success in order to improve that of the hive as a whole (Varju & Núñez, 1993). Without mathematical descriptions of the factors involved, behavioral scientists would not have been able to distinguish between these hypotheses. Moreover, the models pointed to what had to be investigated empirically in order to understand this aspect of foraging behavior.

In the example above, models helped explain a trait that had already been observed in bees, namely partial loads. But *what if the animals do not perform the behavior the model predicts?* Animals may not be optimally adapted, and any studies trying to identify the adaptive function of a trait or behavior are sometimes criticized as being *adaptationist*, that is, naïvely assuming that

evolution will be able to lead to perfection (Gould & Lewontin, 1979). However, this is misunderstanding the aim of such models. First, without quantitative models, we would not be able to determine whether a particular behavior in fact is the one that, given certain constraints, is most likely to allow the animal to reach its goal. Second, models help in defining the problem (the constraints and the goal) more sharply (Stephens et al., 2007). *What is the "goal" of any animal behavior?* The behaviors that are most likely to persist in a population are those that allow individuals to contribute maximally to the genetic makeup of the next generation, largely by maximizing the number of offspring produced. This is what we call **evolution**. There are many components to this—finding and selecting a mate, avoiding predators and diseases, finding shelter or otherwise dealing with the elements, and in many cases establishing a place in a social community (Davies et al., 2012). But for many animals, the amount of food collected is a limiting factor in how many offspring can be produced. This means that behaviors that allow an animal to collect more food often have a direct effect on **fitness**, enabling researchers to employ the shorthand of using "food collected" or "food collected per time" as so-called **fitness proxies**, that is, as the currencies that animal behavior is adapted to maximize (Ydenberg & Hurd, 1998). Indeed animals perform behaviors that we can only understand as strategies to increase foraging success by just a few percent points; the existence of such behaviors shows that evolution can lead to subtle adaptations and optimization. It is important, however, to recognize the limitations of such fitness proxies—primarily, that other aspects of the animal's life are ignored for the purpose of a particular study.

If an animal appears to behave in a way very different from the predictions of a model, this may mean that the animal has not yet evolved the optimal behavior. However, in many cases, it is likely to mean that we have not yet properly understood which problem the animal is trying to solve: we may not understand the **constraints** under which it is operating, or we may not know the **currency** being maximized—for example, perhaps the animal needs to avoid predators or attempts to find mates while foraging (McArthur et al., 2012). Researchers now also study how the computational mechanisms that enable animals to choose behaviors themselves evolve (McNamara & Houston, 2009; Fawcett et al., 2012a, 2012b). For example, this allows us to understand predictable mistakes that result from applying a rule of thumb that provides the best results when averaging over the situations the animal commonly finds itself in but that may not appear optimal in a particular situation, or laboratory experiment (Kamil & Roitblat, 1985; Stephens et al., 2004; Seth, 2007; Houston, 2009). Interestingly, behaviors that are identified with such mental

states as optimism, disappointment, and impulsivity may be interpreted as resulting from such rules of thumb—more on this below.

THE FORAGING TRIP

A honey bee leaves the hive to search for flowers that may provide nectar. The bee starts this trip because she is old enough, has a genetic predisposition to nectar foraging, and has sensed some commotion near the hive entrance, a likely indication that some of her nestmates are already foraging successfully. She (all honey bee workers are female) flies to a stand of cherry trees about a mile from the hive, using her knowledge of local landmarks to find them. Although she foraged successfully from these trees a few days ago, their bloom has faded and the bee starts searching elsewhere. Relying on her innate preferences, she picks some blue wildflowers, but they either do not contain nectar or it is too deep for her to reach. After each unsuccessful attempt, she travels a bit further until she can taste the sweet sugary nectar in some yellow flowers on a meadow. After first locating nectar, she changes her travel path to a more meandering one, testing every yellow flower but bypassing flowers of other colors or shapes. Many of the yellow flowers are empty, but some contain nectar—never more than a tiny drop, often less than a few microliters. After couple hundred flower visits and having collected about a third of her body weight (although she could carry more than two times as much), the bee returns to her hive. There, she passes the collected nectar on to hive-workers; but since she had to queue to complete this task, she decides not to communicate her discovery but to return immediately to the meadow for another foraging trip.

Foraging behavior has many facets. In an animal as well studied as the honey bee, we know many of the decisions made and the factors that will affect them. In bees, early naturalists as well as modern behavioral scientists have studied the factors that prompt bees to start and stop foraging trips, choose or reject certain flowers, navigate away from and back to their nest, and communicate with their nestmates to affect their foraging behavior in turn. I will discuss each of these aspects of foraging separately below.

TO FORAGE OR NOT TO FORAGE

At each trip or bout of foraging activity, an animal has to make several decisions, starting with whether to attempt to collect food at all, or when to do so. This, as any other decision, depends on the benefits and costs of foraging compared to another activity the animal could engage in instead. Benefits of

foraging of course depend on the prospects for success, and many animals innately prefer to forage when cues such as weather indicate that resources will be plentiful. For example, desert ants are sensitive to overheating and will forage only under cool or moist conditions (Cerde et al., 1998). On the other hand, ants can also learn to associate temperature with food (Kleineidam et al., 2007). Many animals learn cues associated with resources, good foraging conditions, or even sophisticated combinations; for example, bees learn not only which areas are most profitable but also at what times of day which locations are most likely to provide food. They can even learn how likely it is that resources will change in profitability, that is, learn when it is worth learning (Dornhaus & Franks, 2008).

Whether a particular animal attends to environmental cues in its decision to forage should depend on how much these cues predict foraging success. For example, the availability of edible leaf material will not change in the short term for a caterpillar sitting on a plant, but the availability of nectar in flowers changes quickly and drastically with the time of day and weather, making it useful for bees to attend to such cues. Whether a particular cue provokes an innate response or is only used after the animal has learned to associate it with foraging success depends on how predictable its effects are over the long term (Dunlap & Stephens, 2009). The life cycle and *circadian rhythm* of specialist cactus bees, which forage on the flowers of a particular cactus, are adapted to the timing of nectar availability in this plant (McIntosh, 2005). The timing of foraging in generalist honey bee foragers, on the other hand, is flexible and is shaped by the bees' experience with the nectar availability of plants in the current season and site. This difference between *specialist* and *generalist foragers* has wide-ranging consequences for species resilience under environmental change.

The benefits of foraging depend not only on the expected returns but also on how the food is used. *Is food necessary to satisfy the immediate energy needs of the animal, is it stored for future need, or is it fed directly to offspring or other individuals?* If food collected is used primarily for *provisioning*, that is, stored or provided to other individuals, then foragers may attempt to minimize energetic expenditure of foraging because any food used up for the foraging activity itself will not be available to provision. When just foraging for themselves, however, animals may behave so as to maximize daily gain without regard for how much is spent attaining it (Ydenberg et al., 1994). For example, the sooty shearwater (*Puffinus griseus*), a seabird, may travel 1,500 km from its nest to catch fish in productive waters to maximize its own energy gain, but when feeding chicks will often perform short trips, which lead to less expensive travel but are less productive (Weimerskirch, 1998).

Do animals ever have “enough food”? The idea that foraging behavior may not so much evolve to maximize food collected as ensure that a certain minimum food requirement is met has been called **satisficing** in foraging research and has been somewhat controversial (Nonacs & Dill, 1993; Ydenberg & Hurd, 1998). It seems obvious from observation that many animals spend a lot of time in inactivity when they could be collecting more food—remember the sleeping lions mentioned earlier in this chapter. However, evolutionary considerations suggest that only if additional food can be converted into offspring or stored as a buffer against lean times, it should be collected regardless of current energy requirements. Indeed, many cases of inactivity are explained by the fact that either another factor limits reproduction in the long term or that current energetic costs of foraging exceed its benefits (Herbers, 1981). For example, there may be limits to the speed with which food can be digested or processed (Burd & Howard, 2005). Alternatively, if there is temporal variation in food availability and food cannot be stored, how many offspring can be raised may be limited by the minimum amount of food that can always be collected; in brief periods of food abundance, an animal would then appear to forage less than expected compared to food availability simply because not enough offspring are present to consume this food. Overall, however, the fact remains that animals vary in the degree to which they display inactivity (Careau et al., 2008) or sleep (Lesku et al., 2009), and that the function of neither is completely understood (Cirelli & Tononi, 2008).

FINDING FOOD

Once an animal has decided to forage, it has to actually locate its prey or food source. The pattern in which animals search is thought to resemble a **random walk**, in which each new step is in a new, random direction. “Correlated” random walks imply that the new direction is affected by the previous direction, usually such that the animal is more likely to keep a straight heading rather than choosing a particular different direction. Even within these assumptions of a seemingly mindless search algorithm, a search path can be optimized for the presumed density and clumping of food sources (Nathan et al., 2008; Sims et al., 2008). However, many animals usually forage in a known area and may return to previously profitable locations or travel along known paths (called **traplines**). For example, bumble bees tend to visit several known profitable flowers in a fixed sequence (Thomson, 1996). These bees are doing multiple foraging trips in a row, and the traplining strategy evens out the time intervals after each flower is revisited. It turns out that this is the optimal strategy for resources that slowly but at a constant rate renew themselves,

such as flowers that typically produce nectar continuously (Ohashi et al., 2007). If a food item has been located by a forager, the forager will often concentrate further search in the same area, a phenomenon loosely termed “win-stay, lose-shift” (implying that if you find something, stay close; if not, shift to another area), a strategy that is optimal if food distribution is patchy in nature (Hodges, 1985).

WHAT NOT TO EAT

Once a forager comes near a prey item, it has to both detect it as a stimulus and decide to attack it. Detection will depend on the foragers’ physiological sensitivity to the color, pattern, smell, or sounds produced by the prey but also on the foragers’ experience and current state of mind. Detecting a stimulus from a noisy scene is often hard; much research in computer science is devoted to trying to replicate the skills of even simple animals in visually recognizing particular items under varying and often patchy lighting, with a noisy background, and from different angles (Smeulders et al., 2000; Galleguillos & Belongie, 2010). In addition, although some food items, such as flowers for bees, actively signal their presence (because flowers are pollinated in exchange for the nectar they offer), others, such as prey animals to be eaten, will be trying to avoid detection. Also, foragers will likely encounter many objects that are either harmful or a waste of time but that resemble the sought prey items. For example, orchids have no nectar but mimic other flowers to fool bees (Dafni, 1984; Gigord et al., 2002), yellow or white crab spiders will camouflage on flowers of the same color (Chittka, 2001), and noxious butterflies may look similar to tasty ones to a bird (Skelhorn & Rowe, 2010; Stoddard, 2012). Foragers thus need to be discriminating and will often evolve particular sensory sensitivity to the most useful stimulus associated with their preferred food (Sabbah et al., 2010). In addition, foragers will often reject items that appear too similar to unwanted items, even to the point of rejecting many suitable ones; this is called the *peak shift* phenomenon in *signal detection theory* (Chittka et al., 2009; Lynn et al., 2005).

If a forager is searching for a particular prey type, it tends to be able to detect items of this type more easily than other potential prey; the forager is said to have a *search image* (Dukas & Ellner, 1993; Dukas, 2004). Why this is the case is not entirely clear, but it may be that even if foragers can recognize several prey types they have difficulty holding more than one in their working memory, where it is readily accessible for comparison with the scene encountered. For example, bees are known to show “flower constancy,” where profitable flowers are ignored in favor of visiting a series of flowers of the same type,

sometimes for an extended period. If a bee switches to a different flower type, it appears to take longer to recognize it. This may reflect the neural costs of accessing information that is not currently in the working memory of the bee (Waser et al., 1996). Several other explanations for flower constancy have also been proposed, however, from the difficulty of learning to handle multiple flower types to avoiding competition with other bees. Indeed, specialization on particular food sources is thought to confer several advantages—ability to specialize on finding, handling, and digesting food as well as savings in cognitive complexity of the forager (Bernays, 2001).

Once a food item has been identified by the forager, the forager is still faced with choices: sometimes among several foods, sometimes between choosing to attack a particular food item now or to ignore it in favor of searching for a better one (Stephens et al., 2007). These choices are referred to as *diet selection* and may be based simply on how long it takes to handle particular food items or on a multitude of factors affecting item quality, including specific nutrients required by the forager (Sih & Christensen, 2001). Animals use a variety of direct and indirect ways to assess the quality of a resource. One of the interesting aspects of this is that the quality assessment appears to be strongly influenced by recent experience: animals exhibit behavior that appears to show disappointment or even optimism and pessimism (Morgan et al., 2012; Nettle & Bateson, 2012). Together, these phenomena have been termed *contrast effects* because they appear when animals experience a contrast between what they have experienced in the past and what they are experiencing now. It is not entirely clear why they occur—after all, if a particular food item is worth more than the effort to handle it, the animal should be using it regardless of whether it is better or worse than expected. However, this is not how animals act. Similarly unexpected, apparently nonoptimal behavior has been shown in other contexts, such as when animals choose a small reward now over a much bigger one later (“impulsivity” [Stevens et al., 2005]), when risky alternatives are preferred or rejected compared to stable ones with the same average yield (“risk sensitivity” [Caraco et al., 1990; Cartar & Abrahams, 1996]), or when irrelevant options bias choice (“irrationality” [Shafir et al., 2002]). New research is now uncovering the actual cognitive mechanisms, or *decision rules*, that animals use and how they have evolved. Often, particular decision rules evolve because they usually, across environments or stimuli typically encountered by a particular type of animal, function well; this does not mean that they provide optimal solutions in all contexts (Houston et al., 2007; Fawcett et al., 2012b). Contrast effects, impulsivity, risk sensitivity, and irrationality may be examples of such rules—for example, animals adapted to catching flighty insects may be more impulsive than those using stable

resources such as plants (Stevens et al., 2005). In addition, previous experience allows the animal to assess its own state as well as that of its environment, allowing better prediction of what is likely to be experienced in the near future (Schuck-Paim et al., 2004). This provides an intriguing angle to view human emotions: *are our irrational-seeming reactions in some contexts the result of evolved decision rules* (Bateson et al., 2011; Nettle & Bateson, 2012)? Many of the insights on diet selection, or how animals judge whether to use a particular resource, also apply to contexts other than foraging, for example when selecting mates; very similar models are also used for humans. For example, models in *sequential choice theory* calculate whether a prey item of a particular quality and taking a particular time to handle and digest should be chosen depending on what other items the forager is likely to encounter later (Stephens et al., 2007); the same models can be used to predict whether an animal should choose a mating partner of a particular quality (given the distribution of potential mating partners) (Castellano et al., 2012) and can also be used to calculate whether a person should take a job offered based on what he or she estimates will be offered in the future and other problems of this nature.

Choices while foraging are also affected by other aspects of an animal's life, such as the risks of encountering predators, mates, or competitors (McArthur et al., 2012; Wajnberg, 2012). Animals are almost always vigilant to avoid a predator attack and often switch between looking for food and surveying the area for possible threats. If the probability of being attacked is higher in particular patches, animals demand "hazardous duty pay" (Brown & Kotler, 2004); in other words, such patches have to be particularly profitable to be visited by a forager. Another aspect is that some areas may be safer, for example if they provide more cover, and will be preferred in the presence of predators; this can lead to changes in overall food use, as in deer who avoid open aspen stands when wolves are present in the area (Fortin et al., 2005). Similarly, animals often avoid competition with individuals of the same or other species. This may be achieved, for example, by specializing on a subset of the suitable foods or by restricting activity to particular times. Dominant individuals or species will then often forage during the most profitable times and on the most profitable sources, while others may be displaced to suboptimal ones (Alanara et al., 2001). For example, in desert ants foraging on cacti for nectar (from *extrafloral nectaries*; see below), the less dominant species forage later in the day, at higher temperatures, putting them at higher risk of dehydration and overheating (Morris et al., 2005).

When a forager ends its foraging bout or leaves a patch of resources, it may then return to its nest to unload and start a new foraging bout or turn to other

activities. If it does this after every trip, it is central-place foraging (Orians & Pearson, 1979); other animals have no fixed home base and instead roam widely within a home range or over large distances (Hays et al., 2006). When to stop foraging in a patch is a decision that depends largely on how the rate of acquiring food from the patch changes over time and how long the forager has to travel between the food patch and its home base. If the food source provides *decreasing marginal returns*, that is, it becomes harder and harder to extract food, the forager will eventually leave it to find a new, fresh resource, possibly well before it has collected all it can (see discussion on partial loads above). How foragers navigate the route back to their nest or among foraging patches is another interesting research area that is discussed in Volume 1, Chapter 12.

EXTRACTING REWARD

So far, we have mostly discussed how to find and recognize food and how to decide whether to attack it—whether it is a prey animal or a plant or anything else. However, actually capturing the prey and extracting the food reward can be a challenge in itself and may be a stereotyped behavior or exhibit a high degree of innovation; it may also involve sophisticated behavioral sequences, whether innate or learned. Consider the emerald cockroach wasp (*Ampulex compressa* [Fouad et al., 1996; Libersat, 2003]). The wasp needs live but subdued insect prey to feed to her developing offspring. The female will hunt for cockroaches and, once they are found, sting into the brain of the roach precisely in the suboesophageal ganglion. This, apparently, turns the roach into the wasp's puppet zombie! The roach appears to lose all will of its own and is guided—live and able to walk—to its doom in the form of the wasp's nest and her larvae (Libersat et al., 2009). This foraging strategy on the part of the wasp is not only surprising and unique, it is also fairly complex but very likely completely genetically determined. Many other animals, on the other hand, have been shown to learn, and even pass on to others in a type of *culture*, particular foraging strategies useful in a local area (Volume 1, Chapter 4). For example, dolphins off the coast of western Australia have been shown to harvest cup-shaped sponges to use as a “glove” over their sensitive snouts when digging on the sea floor (Krutzen et al., 2005); great tits (*Parus major*) famously learned to open milk bottles with aluminum caps left on British doorsteps (Fisher & Hinde, 1949; Lefebvre, 1995); and apes such as chimpanzees and orangutans have been shown to master a variety of tool-using techniques in foraging, from cracking nuts with wooden hammers and anvils to fashioning spears for hunting monkeys (Whiten et al., 1999; van Schaik et al., 2003). *Why do some animals have such sophisticated, flexible foraging*

strategies? It was long thought that carnivores, hunting for live animal prey, needed to be particularly clever and perhaps had evolved more cognitive and sensory abilities as a result. However, the evidence for this is not clear (Garamszegi et al., 2002). On the other hand, it seems that innovative foraging behavior enables some animals to invade new habitats more easily (Sol et al., 2002).

SOCIAL FORAGING

Many animals do not just rely on their own skills and experience to find and identify palatable and profitable food sources (Galef & Giraldeau, 2001; Laland, 2004; see also Volume 1, Chapter 4). For example, many birds will closely watch others in the flock searching for seeds on the ground; if another bird appears to have found something, they will then quickly join it to exploit that same resource. This strategy has been termed “scrounging” (as opposed to “producing,” which refers to birds searching for food themselves) (Giraldeau et al., 1994). Bees may also watch conspecifics choose flowers and instead of attempting to use the exact same flower may use this *public information* to pick other flowers of that same color (instead of using *private information*, or sampling many flower types themselves to determine which species provide the most nectar) (Leadbeater & Chittka, 2007). Rats are known to learn the scent of palatable food from the smell at the mouth of other rats, enabling them to quickly spread information about novel food types in their group (Galef, 2009). Cliff swallows, and other birds that nest in large groups, will watch for other birds returning with a mouthful of insects; if they spot one, they will follow it out to the presumably profitable hunting grounds (Brown, 1988). If information is exchanged at a nest site or colony as in this case, the colony is referred to as *information center*. In all these examples, individuals are using *cues* gained simply by observing behavior of other foragers; the producers of that information do not behave in such a way as to improve the information exchange. However, many cooperative group-living animals also purposefully exchange information in the form of *signals* (Seeley, 1998): honey bees signal the direction and distance of flower patches in the “waggle dance” (Gruter & Farina, 2009), some ants lay pheromone trails to lead nestmates to food sources (Hölldobler & Wilson, 1990), other ant species *teach* (facilitate learning by others at a cost to themselves) their nestmates the route to food by leading them in a tandem run to it (Richardson et al., 2007; Hoppitt et al., 2008). Highly cooperative groups may also improve their foraging efficiency in other ways, such as by employing division of labor (Powell & Franks, 2006; Burns & Dyer, 2008); sometimes this even occurs in non-cooperating groups (Giraldeau & Lefebvre, 1986).