
I.7

Foraging Behavior

Joel S. Brown

OUTLINE

1. Foraging behaviors, adaptations, and autecology
2. Finding food
3. Handling time
4. To eat or not to eat?
5. Patch use
6. Social foraging
7. Fear and foraging
8. Coadaptations between foraging behaviors and morphology
9. Nutrient foraging in plants

A need for energy and resources for survival, growth, and reproduction is a universal property of life. Hence, all organisms must forage. Even plants have noncognitive foraging behaviors. Life exhibits a wonderful diversity of feeding behaviors and associated morphological and physiological adaptations. Food must be found and handled. Letting the food come to the forager (sit and wait) or actively seeking food items (active pursuit) are two tactics for finding food items. Handling a food item may be as simple as absorption (endocytosis by a single cell organism) or a complex choreography of subduing, dismembering, and/or digesting a prey. Diet choice involves foragers deciding which food items to accept or reject. Patch use considers how thoroughly a forager should deplete the food from a spot before giving up and moving to a fresh spot. Foraging often occurs socially because groups permit sharing of information, scrounging, group hunting, task specialization, and, most often, safety in numbers. Predation risk and fear loom large in foraging, as animals balance the conflicting demands of finding food while avoiding becoming food themselves. All of these topics of foraging behavior become central to understanding an organism's ecology and evolution.

GLOSSARY

diet choice. The decisions made by foragers regarding which encountered food items to consume and which to reject. The abundances of different food

types, their ease of finding and handling, and their value to the forager generally influence the decisions to eat or not to eat.

foraging games. The behavioral challenges facing both predator and prey when the prey can perceive and respond to the hunting tactics of the predator, and the predator can perceive and respond to the anti-predator tactics of its prey. These can be as straightforward as pursuit-evasion games; or complex sets of decisions summed up by when and where to forage; or levels of prey vigilance and predator boldness. Finally, foraging games such as producer-scrounger games or behaviors involving territoriality and interference may occur between members of the same species.

nutrient foraging. The noncognitive foraging behaviors of plants as they adjust allocations to roots and shoots, alter uptake kinetics or growth forms to influence the uptake of water, light, nitrogen, and other nutrients.

patch use. The behaviors of foragers regarding how to deplete the food items of a given spot. Most importantly, when should the forager leave an area with food before moving to a fresh area? A forager should leave a depleted food patch when the benefits of continuing to harvest the patch no longer exceed the sum of metabolic, predation, and missed opportunity costs of foraging.

social foraging. When feeding occurs as groups of the same or different species. Social foraging may allow for information sharing, producer-scrounger games, group hunting, task specialization, and very often safety in numbers. Safety in numbers occurs through the many eyes, dilution, and confusion effects.

1. FORAGING BEHAVIORS, ADAPTATIONS, AND AUTECOLOGY

An animal's ecology can be summed up as follows: where does it live, what does it eat, and who eats it? For instance, on the sand dunes of Bir Asluj in the Negev

Desert of Israel, afternoon winds blow in from the Mediterranean, redistributing the sand and uncovering seeds. At sunset, as the wind abates, Greater Egyptian sand gerbils (*Gerbillus pyramidum*) emerge from their burrows and move under shrubs or across open spaces to search for seeds. A knowledge of where seeds likely aggregate guides their search paths. With a keen sense of smell, gerbils hone in on patches of seeds or seeds buried under the sand. With its forepaws, the gerbil recovers seeds and lifts them to its mouth, either transporting them in internal cheek pouches or deftly husking them with practiced coordination of forepaws and incisors. While the gerbil seeks food, predators seek the gerbil. A gerbil's ears and auditory system can detect the low-frequency sounds of a barn owl's wingbeat. A gerbil's quick reactions may save it from the strike of a horned viper, and erratic locomotion permits escape from a pursuing red fox. With cheek pouches full, the gerbil returns to its burrow and deposits the seeds underground in its larder, or it may save time by burying the seeds in a shallow depression, contributing another snack to its scatterhoard. Perhaps another gerbil will pilfer this cache before the owner returns for it. As the night draws on, the gerbils deplete the available seeds and conclude the night's foraging. Most will return to their burrows to await another wind and another night. A few will have fed the predators. Central to the gerbil's ecology are its foraging behaviors and the foraging behaviors of its predators. These behaviors have been engineered by natural selection through the circumstances of making a living as a seed-eating desert rodent. As a result, feeding behaviors are often the most frequent and tangible expression of an organism's ecology.

Feeding behaviors, as products of natural selection, emerge from all organisms' need for energy and resources to sustain life, permit growth, and allow for reproduction. Foraging behaviors are as diverse and varied as life itself. We may describe them in broad brushstrokes such as a sperm whale diving 400 m beneath the waves and submerging for over 40 min as it somehow seeks giant squid. Or these behaviors can be described in fine detail as the exact path and number of steps that a browsing white-tailed deer takes as it moves from one specific shrub to another, stopping to nibble particular leaves from particular branches. Each bite may necessitate some number of chews before the masticated mouthful is swallowed. The precise choreography of step, bite, and chew continues for hours. But in each case, the foraging behaviors can be seen as contingent responses to environmental opportunities and hazards. As behaviors, we can describe the animal's repertoire of specific actions that it uses to find and harvest food. As adaptations, we can ask why did

the whale dive to a particular depth and spend a particular time? Why did the deer favor some leaves over others? Was it the leaves' nutrition, the presence of spines, or plant toxins?

In what follows, we explore both of these aspects of foraging behaviors—the sequence of actions required to get food and the adaptive nature of feeding behaviors. Change the organism, and the suite of available behaviors likely changes too. The exact behaviors available to a single-cell *Paramecium* are literally worlds apart from that of a web-building spider. Change the environment, and the behaviors of a given animal may change dramatically. Bream, a common fish of northern European lakes, can opt to snatch zooplankton from the water when available, or they can probe for tasty detritus in the muck of the lake's bottom.

Here, the focus is on the categories of foraging behaviors and scenarios and the concepts that permit general understanding of foraging behaviors as adaptations. Animals decide where to forage. This topic is covered under Habitat Selection (chapter I.5). Once an animal is searching for food, the sequences of activities alternate between finding food and then handling food. The forager, as it finds and harvests food, faces decisions of “to eat or not to eat” and when to give up a food patch (patch use) as it depletes. One often imagines solitary foragers going about their business peaceably, but social foraging and fear and foraging recognize how foraging can occur in groups and occur under the threat of predation. Through coadaptations of foraging and morphology, there is a wonderful evolutionary feedback between adaptive feeding behaviors and the other physiological (see chapter I.2) and morphological traits of the species. Finally, plant nutrient foraging examines the noncognitive behaviors of plants to access nitrogen, phosphate, light, and water. Throughout, foraging behaviors emerge as adaptations (MacArthur and Pianka, 1966; Emlen, 1966) that permit organisms to acquire food and resources quickly, efficiently, and/or safely.

2. FINDING FOOD

The chemical reaction involving the polymerization of atoms and molecules is limited by the concentration of molecular building blocks and the rate at which these building blocks can be “found” and “consumed” by the growing polymer. Such was the foraging behavior of the first replicators at the dawn of life on Earth, as partially autocatalytic reactions built combinations of proteins and/or nucleic acids. Brownian motion within an aqueous solution allowed these protolife forms to find food. Three billion years later, finding food looms large in all sequences of foraging behaviors. Active-

pursuit and sit-and-wait tactics provide two evolutionary strategies for finding food. Single-cell archaeobacteria and other prokaryotes likely evolved to be either free-floating or attached to stone surfaces.

A sit-and-wait strategy demands less energetically and physiologically of an organism. It generally takes the form of filter-feeding small food items or ambushing large prey items. For it to work, the food must move, either passively as food particles within a water current or actively as mobile prey. Caddisfly larvae attached to stream pebbles extrude a mucus to which food particles become stuck. Many clams buried in the mudflats of the intertidal create their own water current by “siphoning” water through a tube, past a filter-like organ, and then back into the water column. Because the gerbils thoroughly scour the sand dunes each night for seeds, the horned viper can remain motionless, coiled, and ready to strike. Sit-and-wait foraging tends to promote foraging efficiency (reward per unit cost) over foraging speed (captures per unit time).

Mobile foragers that actively seek and pursue their prey generally enhance speed at the expense of foraging efficiency. Sessile or slow-moving food strongly selects for actively moving and searching foragers. Gerbils must go find their seeds, as their seeds do not find them.

The encounter probability (units of per time) is a key foraging parameter. It describes the likelihood of a searching forager encountering a given food item. The encounter probability depends heavily on the forager’s senses. Vision, smell, touch, pressure sensors, hearing, and even cuing in on electromagnetic distortions provide tools for encountering prey. Then there are the cues emitted by the food items or prey. Together, the senses of the forager and the cues of its food determine the forager’s detection radius for food and its likelihood of accurately sensing the food item. For gerbils, smell may provide a detection radius of ~ 10 cm with touch concluding a successful encounter. Larger seeds are easier to detect than smaller seeds, and with humidity, seeds become more odiferous.

Random search is the simplest case where a feeding animal’s likelihood of encountering any given food item is constant and independent of the total number of prey. This idealized condition becomes distorted when predators can observe the distribution and abundance of many food items in advance. A hummingbird moving among flowers or a black rhinoceros among acacia trees can be a “traveling salesman” and map a best route for collecting the food items—they can do better than random encounter. More prey items can enhance the encounter probability by drawing the forager’s attention, or it may challenge the forager with a confusion effect as multiple prey flee haphazardly at the predator’s approach. Finally, the prey themselves may

alter and distort encounter probabilities through camouflage, deception, and even direct signals to the forager that it has been detected. With aposematic coloration, dangerous or unpalatable prey (bees, monarch butterflies, coral snakes) communicate their unsuitability as food items. Conversely, red flowers and intensely colored fruits attract the attention of hummingbirds and robins, respectively.

3. HANDLING TIME

Handling time describes the effort and activities required to harvest an encountered food item. In its simplest form, handling time can be the fixed time required for a gerbil to husk and consume a seed. More generally, it includes all of the effort required to subdue (if necessary), transport (if not consumed on the spot), prepare, and ingest the food. In animals such as a python or a ruminating antelope, handling time can also include a digestive pause that precludes searching for and handling additional food items. In gerbils, handling time may include caching behaviors. An emperor penguin’s handling effort can include marching to and from the colony to provision young.

For predators, encountering the prey may be much easier than actually capturing it. Stanley Temple (1987) recorded how a red-tailed hawk had success rates of 28%, 18%, and 12% when initiating a strike on eastern chipmunk, cottontail rabbit, and eastern grey squirrel, respectively. Predators have additional foraging behaviors of stealth, pursuit, and tactics for killing the prey while avoiding injury themselves. Barn owls attacking gerbils appear to use hearing to encounter and initiate a strike while using vision to enhance the accuracy of the final impact.

The handling behaviors of many foragers may include preparing the prey for consumption and choosing which bits of prey to consume. The gerbil can facilitate digestion by first husking and chewing each seed. Sparrows may “whirr” the wings off insects before ingesting them. If handling is time consuming, such as for a squirrel consuming a hazelnut, the forager may carry the food item to a safer, more comfortable setting. The animal recoups its preparation time by speeding digestion and increasing the efficiency of assimilation. Partial prey consumption, such as a scorpion consuming only the yummier parts of an isopod (sowbug), increases the quality of the ingested food.

If small glass beads are mixed into a pile of seeds, a gerbil will harvest and pouch some of these beads along with the seeds. When licking up termites, an aardvark may consume more dirt than termites. Situations arise where there may be no advantage to taking the time to discriminate between good and bad food items.

Foragers will forgo recognition time when undesirable items are few and far between, relatively harmless to consume, hard to discriminate, and time-consuming to separate. Otherwise, foragers will invest time to distinguish among potential food items.

Handling time can be as simple as the time taken to consume an item or a sophisticated choreography of time, effort, and risk. For a mosquito, handling time begins when the humming of its wings stops as it alights on your skin. She seeks a promising capillary bed within which to insert her proboscis. She injects a bit of anti-coagulant (with luck, free of malaria!) and begins the process of gorging her stomach. All the while, she aims to avoid your wrath should you awake and claim her life.

4. TO EAT OR NOT TO EAT?

Diet choice is one of the fundamental consequences of adaptive feeding behaviors. Organisms do not consume different foods in direct proportion to their abundances in the environment. Feeding animals always appear more or less selective. Diet-choice studies show how foraging behavior results in a triaging of what is available to what is actually consumed. In all cases, the mapping of food availability into diet involves aspects of finding and handling food.

Ronald Pulliam (1974) developed a classic model of diet choice based on the simplest assumptions of random search (constant and fixed encounter probability) and constant handling time. Search is undirected in the sense that the forager does not know what food type it will find until it stumbles on a food item. While searching, the forager cannot alter its encounter probabilities for one food relative to another (search images allow foragers to do this). To the forager, a food type can be characterized by the encounter probability, a , its abundance in the environment, R , its handling time, h , and its energetic value, e .

Even this simple model suggests quite a bit. For instance, the likelihood that the next encountered food item is food 1 as opposed to food 2 is $a_1R_1/(a_1R_1 + a_2R_2)$. The forager should prefer the food with the higher energy-to-handling-time ratio. So, food 1 is preferred if $e_1/h_1 > e_2/h_2$. To maximize its feeding rate, the forager should always consume its preferred item. But should it consume the less-preferred food? The answer is straightforward and simple. If the energy gain from handling an encountered item of the less-preferred food, e_2/h_2 , is less than what could be gained from searching for and handling a preferred item, $e_1a_1R_1/(1 + a_1h_1R_1)$, then the forager should be selective. Otherwise, the forager should be opportunistic and consume all encountered items.

This model and its many variants suggest how animal diets represent a biased sample of availability. If the forager actually rejects consuming less-preferred food items, then diet choice is an extreme all or nothing. Increasing the abundance of its preferred food should cause the forager to reject less preferred items. A bountiful environment encourages picky eaters.

When a forager is opportunistic and consumes all encountered food items, it will have a diet that appears to favor those foods that are easier to find (higher encounter probabilities). Cryptic foods will be under-represented, conspicuous foods overrepresented in the diet. This is why gerbils will harvest a greater fraction of the large seeds than the small seeds from a given patch of sand. This effect of encounter probability on diet explains why flowers and fruits have evolved to be conspicuous (it is adaptive to be harvested) and why moths, stick bugs, and other prey have evolved camouflage (it is nonadaptive to be eaten).

Biases in diets can result from foods occurring in separate patches or habitats. When foods occur apart, search is no longer random with respect to food type. It is now directed toward one food or the other, but not both. The forager may appear to favor one food over another simply because that food occurs in particularly rich patches or safe habitats.

The state of the forager may alter its diet choice. For a mountain lion, mule deer are hard to encounter and successfully capture, but they pose minimal risk of injury to the mountain lion. Porcupines are the opposite. They are easier to encounter but they pose greater risks of injury to the mountain lion. Hence, a well-fed, successful mountain lion should eschew porcupines. But a down-and-out mountain lion should prefer to try its luck on capturing a porcupine rather than succumbing to the certainty of starvation. Bruce Patterson (2004) and others note this factor in the foraging behavior of large, man-eating cats. The man-eating lions of Tsavo likely switched diet as a consequence of prior crippling injuries.

Nutritional relationships—substitutable, complementary, antagonistic, and essential—among foods can loom large in diet choice. Foods may offer different essential or complementary combinations of carbohydrates, fats, proteins, minerals, and vitamins. Shy on salt, moose of the northern Great Lakes of North America favor a salt-concentrated plant. Moose along coastal Scandinavia lose interest in this plant because much of their diet automatically includes plants impregnated with Baltic sea salt. A balanced diet means that foragers appear to favor the rarer food type or the food type with the scarcer nutrient. This balancing of nutrients can apply to plant toxins as well. Different plant species defend themselves with different chemical

toxins such as tannins and oxalates. To an herbivore, it may be better to consume some tannins and some oxalates rather than a lot of just one—dose makes the poison, and feeding animals will often include this fact in their foraging behaviors.

5. PATCH USE

A jar of peanut butter or jam becomes increasingly frustrating and unsatisfying as the contents deplete. When full, a single swipe of the knife yields a bountiful spread. When mostly depleted, repeated strokes of the knife yield paltry returns. Eventually, we give up and discard the jar even though some contents remain. We share this dilemma of when to give up a depleted food patch and seek another with almost all feeding animals. Food items generally occur patchily, and the rate of food harvest declines as the patch becomes depleted. At what point should the forager abandon the patch, and how much unharvested food will it be leaving behind?

Eric Charnov (1976) proposed the Marginal Value Theorem for how long to remain in a food patch. The forager should leave its current patch when its harvest rate within the patch no longer exceeds what the forager's average harvest rate would be from leaving this patch, traveling to a fresh patch, and foraging that patch to the same quitting harvest rate. Put simply, leave a patch when the marginal rate of return (current harvest rate) drops to equal the forager's average harvest rate from the environment at large.

A forager should spend less time in a poor patch than a rich patch; a forager should spend less time in a patch of a rich environment than a poor environment; and a forager should leave patches sooner when travel time between patches is less. Foragers generally conform to these predictions, but with caveats. The costs and benefits of patch use may be more varied, and this has inspired variations and extensions of Charnov's model.

More generally, a forager should remain in a food patch until the benefits of harvesting resources, H , no longer exceed the sum of metabolic, C , predation, P , and missed opportunity, MOC , of foraging. Leave a patch when the harvest rate drops to $H = C + P + MOC$. If the forager's harvest rate within the food patch is directly related to the remaining abundance of food within the patch, the animal's patch use strategy also results in some amount of food being left behind. This remaining amount of food is referred to as the "giving-up density." The size of this giving-up density should be proportional to the animal's perceptions of foraging costs.

The gerbils of Bir Asluj demonstrate how giving-up densities change with these foraging costs and benefits.

Gerbils have lower giving-up densities on foods that are more valuable, on foods that are easier to find, and within food patches that offer higher encounter probabilities on foods. Cold nighttime temperatures raise the gerbils' metabolic rates (C), and consequently they have higher giving-up densities on cold nights than warm nights. Gerbils feel safer (P) and have lower giving-up densities when seeds are under shrubs than a few meters away in the open, and they have lower giving-up densities on nights with no moon than with full moon. When resources are abundant within the environment (MOC), or when the gerbil has large stores of food, it will forage to a higher giving-up density and exaggerate its avoidance of the risky, open microhabitat even more. Well-off animals have more to lose from being killed by predators than animals in low states of energy or well-being.

The ability of foragers to detect and respond to variability in the distribution of food among patches is important for their ecology and their foraging behaviors. Perfect information on food availability allows the animal to perfectly balance its foraging time toward rich and/or safe food patches. Poor information on patch quality leaves the forager spending too much time in poor patches and too little time in rich patches. In reality, animals use sensory cues to "visualize" and assess patch qualities before investing time in the patch. Additionally, the foraging animal can use its experience within the patch to estimate patch quality. If the forager is having an easier time finding food than it expected, this may indicate a higher than average food abundance. Bayesian foraging studies how animals can use prior expectations and current experience to form an estimate of patch quality. The actual patch use behaviors of animals suggest that few have perfect information. Rather, foragers use a combination of pre-harvest sensory cues and sample information while foraging to form and update their estimate of patch quality.

The gerbils deplete their food patches by actually harvesting the seeds. But for foragers that have prey that can run, hide, or become vigilant, patch use takes the form of behavioral resource depression. The mere presence of the predator causes the "patch" to become less valuable as prey flee or become more wary. For predators with fearful prey, the catchability of their prey becomes as important as the number of prey. Cows in a pasture enjoy a very different proximity to birds than does the Cooper's hawk or Goshawk that aims to capture these birds.

Patch use behavior, through the giving-up density, has important implications for the distribution and abundance of the forager's food or prey. It may be that what we see in nature is simply the residue of feeding

behaviors. What we see may often be what the foragers care not to eat, cannot eat, or cannot catch.

6. SOCIAL FORAGING

Leaf-cutter ants coordinate foraging as ants in the tree canopy drop their harvest to the ground where others transport the leaf discs back to the colony. Hyraxes post a sentinel that allows the other hyraxes to forage less fearfully. To counter these social foragers, one black eagle of a pair may circle in one direction from the colony, permitting the other eagle to fly in from elsewhere and surprise the otherwise distracted colony. Pelicans, seagulls, and cormorants are famous for forming noisy aggregations around promising patches of schooling fishes. These are all facets of foraging in groups. They reveal the competing interests associated with task specialization, predator detection, group hunting, information sharing (or dissembling), and shameless scrounging.

On first inspection, social foraging makes no sense. If a gerbil seeks to comb the sand dunes for seeds, doing so as a group simply means everyone has to walk farther for the same reward. When searching for food, better to divide the space and spread out. Hence, two critical factors loom large in social foraging—the forager's prey is behaviorally responsive, and the foragers fear their own predator. Advantages to social foraging as an antipredator adaptation accrue from having alarm calls, sentinels, many eyes, the dilution effect (better to catch my neighbor than me), and the confusion effect (many fleeing foragers may distract the predator from capturing any one forager).

When prey can flee or react, group foraging may permit task specialization (driving prey into an ambush), the ability to aggregate the prey (dolphins and whales corralling fish), beating the brush (banded mongooses moving abreast to scare up insects), or permitting the capture of large dangerous prey (army ants on vertebrates, wolves on a moose).

Information sharing looms as a benefit and consequence of group foraging. Spotting where others have found food may reduce the entire group's efficiency at finding food, but it may reduce the variance in food consumption. Less successful foragers join the feeding frenzy created by one forager stumbling on a particularly rich food patch. Some animals such as vampire bats and African hunting dogs will regurgitate and share food. Overly satiated members feed hungrier members. Such food sharing can even allow for task specialization where some individuals collect food even as others incubate a nest, protect a brood, or defend a territory from intruders. Of course, information sharing and gauging the successes of others introduces

conflicts of interest where an individual may prefer to scrounge rather than produce its own harvest. Social groups encourage freeloading and producer-scrounger games. It may be that in some groups where siblings help their parents raise offspring (Florida scrub jays, Arabian babblers, and other birds), the balance of the relationship rests on the willingness of the parents to tolerate their "adult" offspring so long as they contribute food for their newest sibs.

Ant and bee colonies represent eusociality, the extreme of social foraging. These species exhibit caste systems, information sharing, group hunting or harvesting, and food sharing. What makes these systems special relative to a wolf pack or a naked mole rat colony? It may be the evolutionary objectives of the foragers that dictate the dividing line between a eusocial system and one that is merely a highly despotic social hierarchy. Individual worker ants and bees have been shown to forage in a way that completely subordinates themselves toward the fitness and success of the colony, whereas wolves and even individual naked mole rats seem to promote their own self-interests tempered by their need to be part of and treated well by the group.

7. FEAR AND FORAGING

Not a section of this chapter has gone by without some role for predators in shaping foraging behaviors. Foragers face a fundamental trade-off between food and safety. This trade-off becomes exacerbated and almost ensured by the adaptive behavior of having higher giving-up densities in risky than safe habitats. In most places and at most times, feeding animals face an environment in which background food abundance is high in risky habitats and low in safe places. A clever forager will use the tools of time allocation and vigilance to balance this trade-off. A clever predator will consider its prey's behaviors when doing its own foraging. The reciprocal behavioral responses of prey and predators lead to studies of predator-prey foraging games. Games of fear and stealth abound in nature across all taxa and ecosystems.

Steven Lima and William Mitchell have described the predator-prey shell game as prey seeking places free of predators and predators seeking to be where the prey are. The environment determines the form of the game. The afternoon winds at Bir Asluj ensure abundant seeds at dusk. This encourages gerbils to emerge early, which encourages clever owls to do the same. The responses of gerbils to seeds and of owls to gerbils create three temporal gradients. The seeds decline steadily as the gerbils deplete them. Gerbils start the night wary of owls and become increasingly less so as

the night draws on. The owls modulate their behavior to track the seeds—busy early and less so later.

Foraging games can encompass several prey and predators. Owls encourage gerbils to forage more under shrubs than in the open. Snakes take advantage of this fear response by lying under shrubs in ambush. Owls and snakes create predator facilitation where the presence of one predator species makes it easier for the other to capture the shared prey. Furthermore, the nightly decline of seeds and risk promotes the coexistence of the Greater Egyptian sand gerbil with a smaller cousin, Allenby's gerbil (*G. andersoni allenbyi*). The size, temperament, and behavior of the large gerbil suits it for early in the night, whereas the little gerbil has adaptations and behaviors more suited to the resource poor but safer periods of the night. Burt Kotler (1984), through "fear and foraging," showed the role of predation risk in the foraging behaviors and coexistence of kangaroo rats and pocket mice at a desert site in Nevada.

The behaviors of the prey may facilitate the coexistence of diverse predators, and the behaviors of predators may similarly promote diverse prey. Nowhere is this more likely than the reciprocal radiation of insects and plants. The feeding behaviors of herbivorous insects select for plant defenses. The evolution of additional insect species to overcome these defenses simply encourages the evolution of additional and more diverse defenses among an increasing number of plants species. So the game of feeding and defending promotes other morphological adaptations and perhaps even speciation and adaptive radiations.

8. COADAPTATIONS BETWEEN FORAGING BEHAVIORS AND MORPHOLOGY

Coral reef fishes offer a bedazzling array of sizes, colors, and shapes. Many of these species feed on corals or the algae that grow in them. Close inspection of these fish reveals delicate differences in the mouthparts, mandibles, and teeth. Like a tray of dental instruments, these varied mouthparts permit the different species to scrape algae from diverse surfaces, chew coral, and probe interstices within the coral for food. The body sizes, fin dimensions, and body forms of the fish serve to stabilize and maneuver the fish within the water column to permit access to food and escape from predators. We see a fine-tuned coadaptation of feeding behaviors, mouthparts, and other morphological attributes. But, what came first—the behavior, the mouthparts, or the body form?

My doctoral advisor Michael Rosenzweig would tell us how "Natural selection can never adapt an organism to something it does not do." A feeding be-

havior must then precede coadaptive changes in physiology and morphology. But the species' prior physiology and morphology must at the very least allow for the behavior. This necessitates an important distinction between behaviors being selective versus opportunistic, and morphological adaptations as being specialist versus generalist (Rosenzweig, 1991).

A feeding animal may be more or less picky in its selection of foods and/or places to feed. A North American robin may choose to feed selectively on insects or fruits, or it may opportunistically feed on both as they are encountered. When the robin is feeding just on insects, its gut modulates to enhance the digestion of insects at the expense of fruit, and vice versa when robins feed primarily on fruits. Finally, the body size and morphology of a robin make it adept at probing for insects in the soil and leaf litter, moderately apt at picking insects from branches and leaves, and quite unable to collect insects from under bark or by "fly-catching" insects from midair.

As natural selection engineers a fit between form and function, feeding behaviors or their absence can have profound consequences for the other traits of an organism. If a feeding opportunity arises, then a species previously nonadapted to this opportunity may acclimate by altering its foraging behavior. As this opportunity becomes an important part of its ecology, there will be selection on the species morphology and physiology to adapt. For instance, the cultivation of apples in the New World led to the apple-maggot fly evolving a new species. The precursor species inhabited native hawthorns. Those that switched to apples were now selected to fine-tune their breeding strategies to better match the flowering and fruiting phenology of apples. As the flip side of this same force, if a forager ceases to have a particular feeding opportunity, the absence of this behavior from its repertoire could lead to the loss of morphological and physiological adaptations aimed at improving the rewards from the now-absent behavior. Conserving a species may require us to preserve environments that maintain its full suite of feeding behaviors.

9. NUTRIENT FORAGING IN PLANTS

Plants forage too. They exhibit noncognitive behaviors and responses to light, nutrients, and water. Their "behaviors" represent allocation decisions and growth patterns. Their architecture and investment into roots contribute water and nutrients. Investment into above-ground leaves and stems influences carbon fixation. When viewed as nutrient foraging, most, if not all, of the principles and concepts of animal foraging behavior apply to plants—often with dramatic effect.

We often take wood for granted. Clearing trees created farmland and pastures. The wood itself could heat homes and power machines. As a building material it is sturdy, strong, and durable. The chair I sit in now is made from maple. Why is there wood? Competition for light. Nutrient foraging for light creates a special form of the tragedy of the commons. To be successful at having full sunlight, a plant need only be a bit taller than its neighbors. But if these neighbors respond in kind, an arms race ensues with ever greater and greater investment in sturdy, tall, woody trunks. What determines the canopy height? The costs and benefits of foraging. The benefit of being in the sunlight remains mostly constant because the available pool of light does not change with height (unless one gets demonstrably closer to the sun!). Yet the costs multiply with ever thicker trunks, greater surface area for pathogens and boring insect pests, greater mechanical challenges of transporting water to the canopy and photosynthates back to the roots, and greater chances of toppling over. As the trees play an evolutionary game of light competition, they achieve a canopy height at which no individual can benefit from being a bit taller and no individual is willing to concede light by being shorter. The environment-specific and tree species-specific adjustments of these costs and benefits produce 80-m-tall redwood forests and 30-m-tall European beech forests.

Other strategies for light foraging abound. Light gaps encourage the lateral growth of branches and strange bends in stalks or stems. Maple trees will produce “sun-loving” leaves for their canopy and “shade-tolerant” leaves for their subcanopy branches. Some plants will track the path of the sun with their leaves. Leaf size, morphology, greenness, and stem structure all contribute to the hugely diverse ways by which plants forage for light. A kind of producer–scrounger game happens when species of vines skip the investment in wood and simply achieve the canopy by growing up another’s trunk.

The same holds for belowground nutrient foraging via roots. Plants may overproliferate roots with the goal of “stealing” nutrients from a neighbor. Of course, the neighbor is selected to respond in kind, and a belowground tragedy of the commons ensues. Roots show other varieties of noncognitive foraging behaviors. Plants will direct root proliferation toward areas of high nutrients. Plants may modulate root architecture (fineness of roots, density of root hairs) and root uptake

kinetics (ability to actively transport nutrients) in response to nutrient opportunities.

The bargaining game between mycorrhizal fungi and plants presents an emerging frontier. Mycorrhizae are adept at concentrating nitrogen and phosphorus and then exchanging these with the roots of a plant for carbohydrates. To what extent is this symbiosis best modeled as a nutrient game? Elevated carbon dioxide levels in the atmosphere pose one of the greatest and most interesting challenges for the twenty-first century. Can nutrient foraging by plants play a role in understanding the dynamics of atmospheric CO₂ and the concomitant climate change? This author thinks so.

Whether animal or plant, universal aspects of feeding behaviors involve tactics for searching for and handling resources, foods, and prey. This process reaps rewards in terms of the value of the harvest and incurs costs that include the risk of injury or predation. The interplay between natural selection and the variety of environmental circumstances produces the myriad of foraging behaviors found among the millions of species inhabiting the planet. These behaviors allow foragers to seek and handle foods quickly, efficiently, and safely. The wind will blow, the seeds will redistribute, the sun will set, and the gerbils and owls will emerge to forage.

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