

A Practical Technique for Measuring the Behavior of Foraging Animals

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Animal behavior is well suited for illustrating ecological and evolutionary principles. For ecology projects or labs, animal behavior has a number of advantages: It is inherently interesting to most students, it can be observed, it is flexible and it can change quickly. Unfortunately, meaningful observations of behavior tend to be time-consuming and difficult to analyze. To overcome this handicap, we introduce an indirect procedure that uses the foraging behavior of animals at experimental food patches to address questions in animal behavior. The data are the food left behind by the animals. Such data are quantitative and easily analyzed using a variety of descriptive or inferential statistics. The experimental procedure encourages students to ask questions relevant to how environmental factors such as climate, vegetation structure and predation risk influence animals' foraging behavior. When several species are included within the study, interspecific differences in behavior provide an easy and relevant introduction to questions of niche separation and species coexistence.

Because it uses food left by animals in feeding patches, the technique does not require hours of observation, handling of animals or expensive equipment. Because feeding is central to all animals regardless of environment, studies can be conducted on school campuses using urban birds (sparrows, doves, pigeons, starlings) or small mammals (squirrels, mice and rats). The cost/benefit theory behind the technique is intuitive and accessible to students. The breadth of be-

havioral questions that can be readily addressed gives students the opportunity to suggest their own hypotheses and experiments. The projects emphasize the methodology of a scientist and, we hope, the excitement that accompanies creative thinking and novel results.

Rationale

"Talking" to animals requires a common language, and feeding behavior can provide just such a language. Mixing food into a substrate creates a food patch and provides a technique for "asking" foragers how they perceive their environment. The food patches are like a survey distributed to the animals being investigated. The animals fill out the survey by digging for and harvesting food from the tray's substrate and then sign these trays with footprints, body marks and other telltale disturbances of the substrate. The amount of food left in the patch contains the answer to the survey.

The following approach to feeding behavior represents evolutionary ecology. From an ecological perspective, two universal properties of life include:

1. Births and deaths
2. The need for energy and nutrients to maintain homeostasis and life functions

From an evolutionary perspective, these two properties of life encourage animals to have feeding behaviors that allow them to acquire food in an efficient manner.

Feeding animals make decisions about where to feed (habitat selection, MacArthur & Pianka 1966), what to feed on (diet choice, Pulliam 1974) and when to quit an area and move to another location (patch use, Charnov 1976). We assume that natural selection has favored those animals whose feeding decisions maximize their fit-

ness (survival and reproduction). If so, an animal should leave a patch when its benefits of continued feeding in the patch no longer exceed its cost of feeding in the patch. The formal framework behind the assertion in the previous sentence is called Optimal Foraging Theory (see Stephens & Krebs 1986).

We begin by elaborating a rule for when an animal should leave a patch and then discuss how this rule can be used to reveal aspects of that animal's ecology. An example from our own work illustrates this rule. We provided kangaroo rats living in the Sonoran Desert of Arizona with shallow aluminum pans (45 x 45 x 2.5 cm) filled with a known amount of millet seed (3 g) that has been mixed into 3 l of sifted dirt. Kangaroo rats foraged enthusiastically in these food patches. As more and more seeds are eaten, the large amount of dirt in the patch makes it increasingly difficult for the kangaroo rats to find the seeds that remain. Therefore, the benefit of remaining in the patch declines. At some density of seeds the cost of looking for the next seed exceeds the benefit derived from harvesting and consuming that seed. At this critical seed density the kangaroo rat should leave the patch. If it continues to forage past this density, it forages at a loss (costs exceed benefits). If it quits early, it forfeits the food that it could have profitably gained.

An animal should leave a food patch when its benefits equal its costs (see Brown 1988 for a formal treatment of the theory). To apply this foraging theory, the animal must experience a declining rate of return from spending time in the food patch, and the animal must experience both benefits and costs from exploiting the patch. The benefit to the forager is its rate of harvest of food times (H) considered in terms of energy or nutrient intake. The costs of spending time in a food patch include energetic costs (E) of searching for and handling food items,

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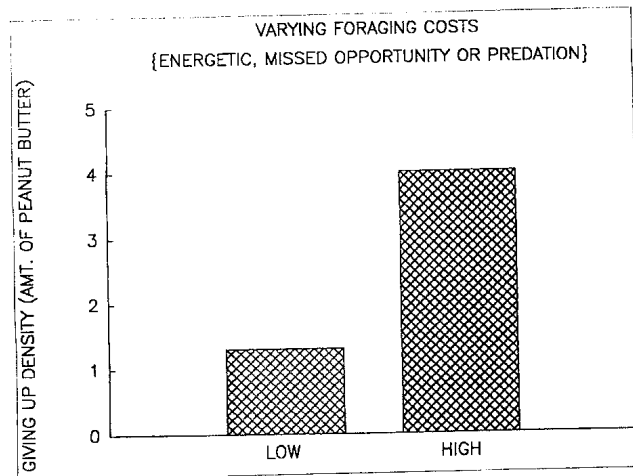


Figure 1. An illustration of how giving up density of peanut butter might vary with experimental conditions. The LOW giving up density relative to HIGH indicates a lower energetic, missed opportunity or predation cost of extracting peanut butter from a jar.

risk of predation (P) and the missed opportunity cost (M) of not engaging in alternative fitness-enhancing activities such as mating, defending a territory or exploiting a richer food patch. The patch-leaving rule can then be written as:

$$H = E + P + M$$

This rule provides the model for investigating foraging behavior. An animal should leave a food patch when the harvest rate from the patch no longer exceeds the sum of the energetic, predation and missed opportunity costs of foraging. In reality, it is difficult to measure H and even more difficult to measure E, P and M in terms of their fitness consequences, which is their true common currency. Fortunately, the density of food left behind in a patch when an animal quits foraging is a good surrogate for H. We refer to this quitting density of food as the Giving Up Density or GUD. All else equal, a higher GUD corresponds to a higher H. For our kangaroo rat work, the weight of millet seeds left behind in patches following a night of foraging (kangaroo rats are nocturnal) measured the kangaroo rat's GUD.

A Useful Analogy of the Rule for Leaving Patches

We have found that the following human example of the patch-leaving rule is useful because it provides students with a mental image of the way GUDs change when the cost components are manipulated. Imagine an almost empty peanut butter jar (this is the resource patch). As you remove peanut butter from the jar it becomes more and more difficult to get the next spoonful out (this demonstrates a declining rate of return). According to the rule, you will quit removing peanut butter when the benefit (the harvest rate) just equals the sum of the costs (energetic, predation and missed opportunity). The amount of peanut butter left in the jar will be your GUD.

Now, what happens when one of the costs is varied while the others are held constant? When it is cold and more energy is required to scrape out the last bit of peanut butter (higher energetic cost), then you will likely leave more peanut butter in the jar (have a higher GUD) than when it is warm. Likewise, if you were removing the peanut butter from a jar while in the middle of a busy street (high predation cost), again you would probably leave more peanut butter in the jar than if you were safely on the side-

walk. And finally, if you knew there was another full jar on the shelf, or that you were missing out on a great TV show (high missed opportunity costs), again you would leave more peanut butter in the jar.

The amount of peanut butter left in the jar, the GUD, is a clear reflection of your perception of these three types of costs. Refer back to the equation and note that if any two costs are held constant, any differences in GUDs between experimental treatments will indicate the effect of the variation in the third cost (see Figure 1 for summary).

Methods

Using GUDs to Study Feeding Costs & Opportunities

The model predicts that two identical feeding patches placed side by side within the same habitat should have the same GUD. This is because both trays have the same substrate and food items (controls for H) are subject to the same microclimatic conditions (controls for E), are equally exposed to potential dangers (controls for P), are equally situated for alternative activities (controls for M) and are available to the same animals (different animals may vary in their perceptions of the food, energetic costs of foraging, predation risk and opportunities provided by alternative activities). The above prediction allows for controlled manipulations of the model's components (H, E, P and M). The effect of any one of the components on the GUD can be tested by holding the other components constant. In what follows it is important to remember that higher GUDs mean more food is left in the patch, hence the animals either perceived higher costs or lower benefits from harvesting the patch.

Consider an investigation of factors that may influence harvest rates. Placing food patches side by side within the same habitat can control for energetic costs, predation risk and missed opportunity costs. By varying food types, food size or substrate, it is possible to test for their effects on H. Larger amounts of substrate or more difficult substrates should increase GUDs. GUDs should be lower on foods that are either preferred or easier to find and handle. For instance, GUDs should be lower on conspicuous food items than on cryptic ones. Such effects can be used to great advantage. The importance of size or nutrients can be tested by seeing how GUDs vary across food items with

different sizes or nutrient contents. The importance of specific sensory modalities to the animal can be tested by comparing GUDs across food items that vary in visual or olfactory cues (foods can be dyed to influence vision or dipped in vegetable oils to influence olfaction).

Consider an investigation of factors that may influence energetic costs. Placing trays that contain the same substrate and foods near each other can control for harvest rates, predation risk and missed opportunity costs. By varying the microclimate among trays, it is often possible to test for the effects of factors such as wind, solar radiation and temperature on GUDs. The experimenter can either take advantage of natural climatic variation that occurs in different habitats or on different days, or the experimenter can use equipment such as fans, artificial lighting and shading, or heating pads and cold packs to perform manipulations of wind, radiation and temperature.

An investigation into factors influencing predation risk can be particularly rewarding. Even animals that experience few predators will respond strongly to manipulations of perceived or actual predation risk. Because of predation's costliness and irreversibility to the victim, a little predation risk can become magnified into large behavioral changes. (Witness the large decline in tourists to countries that experience even minor civil disturbances.) Many animals such as small mammals and birds seek refuge from predators by concealment in vegetation. Hence, predation risk is often greater away from cover than near cover. This can easily be exploited by placing one feeding patch near a tree, shrub, hedgerow or den and placing the other in the open just a few meters away. It is often simple to alter an animal's perception of predatory risk (e.g. scarecrows) by varying visual (facsimiles of the actual predator), auditory (tape recordings of the predator's vocalizations) or olfactory (fur or excrement from the predator) cues. (Ungulates at zoos are known to spend less time feeding and more time vigilant when their cages are near to those of their feline or canine predators). In all cases, increased perceptions of predation risk should result in increased GUDs.

Factors that influence missed opportunity costs are often harder to manipulate in a controlled fashion, but are no less accessible to experimentation. Because an animal's missed opportunity cost is a property of its environment at large and not of a specific

substrate, food or place, manipulations of M must be made across animals or across time. Manipulations of the background abundance of alternative foods is perhaps the most direct way to manipulate missed opportunity costs. As foods become naturally or artificially more abundant in the animal's environment its GUD should increase. By scattering sunflower seeds onto the home ranges of selected fox squirrels we were able to increase their GUDs relative to un-supplemented home ranges.

In summary, the model allows the forager to reveal its preferences and assessments of the environment. Thus, if a squirrel leaves more nuts in a seed tray from the protection of a large tree, it may indicate an increased predation risk. Or, if house sparrows have lower GUDs on warm days than on cold, this indicates lower energetic costs. If pigeons have higher GUDs close to a snack bar, this may indicate that they have a higher missed opportunity cost when other food sources are readily available. Students can investigate any number of species-specific and habitat-specific differences in foraging costs and benefits by holding three of the model's components constant among food patches.

Comparisons Across Species: Using GUDs to Understand Species Coexistence

The competitive exclusion principle—two species cannot occupy the same niche at the same time and in the same place (Hardin 1960)—has challenged ecologists to provide explanations for the coexistence of species that have similar diets and habits: How do ecologically similar species coexist in one area? (Diamond & Case 1986; Ricklefs 1990). A widely accepted view considers how evolutionary tradeoffs in competitive abilities among different species promote coexistence (Kotler & Brown 1988). According to this view, a species cannot evolutionarily improve its ability to exploit a food or habitat without sacrificing its ability to exploit some other food or habitat. In this way, species that are close competitors are able to coexist by specializing on different foods or habitats.

A comparison of GUDs across species can provide insights into the coexistence of competitor species. One measure of competitive superiority is a species' ability to profitably harvest a resource to a low abundance (Tilman 1982). Such a species, by maintaining resource abundances at low levels,

may "starve" other species out of the community. Coexistence is facilitated if each species has a food (or habitat) that it can profitably harvest to the lowest abundance. The GUD of a species on a particular food or within a particular habitat provides this measure of competitive ability. The competitor that is superior at exploiting a patch is the forager with the lowest GUD. It can reduce the resources to a level that cannot be profitably exploited by any other species.

GUDs, by measuring relative competitive abilities, can determine whether patterns of food and habitat use promote coexistence. Within a habitat, coexistence is facilitated if each species has a food on which it has the lowest GUD. Similarly, when there are two habitats, species coexistence is facilitated if each species has a habitat in which it has the lowest GUD (Figure 2).

The senior author has done research with two ground squirrel species that illustrates coexistence via habitat selection. Both species of squirrel feed in open meadows, but the golden-mantled ground squirrel (*Spermophilus lateralis*) has the lower GUD far from the meadow's edge, while the least chipmunk (*Tamias minimus*) has the lower GUD closer to the meadow's edge (Figure 3). Experimental manipulations of cover and predator activity revealed that differences in perceived predation risk generated this pattern of habitat use. The coexistence of these two species is promoted by a tradeoff between anti-predator tactics and the ability to efficiently exploit resources. The ground squirrel is superior at avoiding predators in the more open habitat far from cover, but inferior to the chipmunk at exploiting resources in the absence of predation risk. Similar tradeoffs have been shown to promote coexistence in desert rodents (Brown et al. 1988).

The above study with squirrels shows how a species' perception of foraging costs and benefits influences the use of food patches, which, in turn, promotes coexistence. In particular, predator-mediated habitat selection illustrates a profound effect of predators on community organization that goes beyond the actual capture of competing prey species by predators (usually taught as the "keystone predator effect"). As a result, students can use GUDs in feeding patches to study important effects of predators on their prey without having to observe and measure predation events. In fact, observational studies that focus only on the actual capture of prey by predators probably underestimate the impact of predators on their prey.

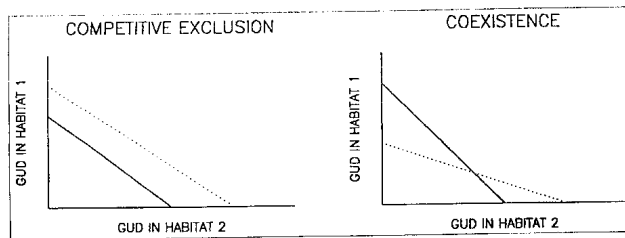


Figure 2. Examples of how two species' GUDs (A and B) in two habitats (1 and 2) may either inhibit or promote their coexistence. In the first figure, species B has the competitive advantage in both habitats and will tend to competitively exclude the other species. In the second figure each species has a habitat in which it has the competitive advantage: Species B is superior in habitat 1 and species A is superior in habitat 2. This arrangement of GUDs will promote species coexistence in an environment that contains both habitats.

Materials & Equipment

The technique of measuring animals' GUDs need require only minimal expenses and can be performed in most outdoor areas. The first steps are to select study organisms and assemble appropriate food trays. Depending on the animal, experiments should be conducted overnight or during the day. Good study animals are those that are abundant and eat stationary prey. Our suggestions for suburban, diurnal animals include: sparrows, pigeons, other seed-eating or fruit-eating birds and squirrels. Good suburban and nocturnal animals include: cats, opossums, mice and raccoons. Native animals in their natural habitats (seed-eating birds, rodents, skunks, foxes, coyotes) also may be ideal for study. We have even seen such experiments with Ibex and porcupines.

Feeding patches consist of a tray filled with a food mixed into a substrate. Feeding trays can be baking pans, cardboard beer or soft-drink flats (free at most grocery or liquor stores) and buckets, or feeding trays can be constructed from materials such as sheet aluminum. The substrate within the trays can be wood fibers, straw, gravel and artificial turf. As a substrate we favor sand or sifted dirt because of the ease of recognizing the animal's footprints. In sand it is often possible to distinguish among the spoor of animals such as large and small mammals and birds. The appropriate food depends on your choice of animal. The food should be attractive to the animal, easily available from grocery, pet or feed stores and of a

particle size that yields measurable GUDs. We have found that millet seed is good for seed-eating rodents and birds. We have also used peanuts, sunflower seeds, mealworms and various types of commercial animal chow.

Some preliminary work must be done to establish the amount of substrate and food necessary to attract foragers and to insure a declining foraging rate (they must leave some food items or you will have nothing to measure). The design of the trays might be part of a project that tests student ingenuity (see Table 1 for guidelines on choosing materials). We have successfully used aluminum pans (45 x 45 x 2.5 cm) filled with 3-10 g of millet seed mixed thoroughly into 2-3 l of dirt or sand as feeding patches.

Retrieving and measuring the remaining food within a patch usually requires a sieve of an appropriate size to separate food particles from substrate material (we use a screen mounted on a wooden frame), a tub or large bag to catch sifted substrate and small plastic bags to hold the remaining food items from each patch. (We place a data tag with information on date, tray location, treatment and footprints into each bag as it is collected). Finally, a table is needed on which to do final food sorting (often the remaining food items need to be separated from debris that still remains following sifting) and a balance or volumetric cylinder to measure the GUD (the amount of food left behind). To minimize recording errors, we write the GUDs on the back of each tag before transferring data to data sheets.

Design & Implementation of Experiments

Placement, number and replicates of food trays depend on the hypotheses to be tested. This is an excellent opportunity to involve students in experimental design. Paired treatments (such as one tray in the open and another near cover) are the simplest to analyze. Begin each trial by evenly mixing a measured amount of the food item into each tray. Allow the foragers to move freely between the trays. The investigator does not have to observe the trays; in fact, it is usually best to leave the area entirely, since the presence of an observer acts to heighten perceived predation risk. The bout is over when foraging ceases (end of day, night or other activity period). When collecting data, note any footprints in the sand or dirt, as these indicate when species left the tray last (this allows for proper attribution of the GUDs if comparisons between species are to be made). Remove the unharvested food items from the trays, usually by sifting them out of the substrate. In many cases, further sorting by hand will be necessary to

Table 1. Attributes of trays, substrate and food items that should be considered when designing experimental food patches.

Trays

1. Deep enough to prevent excessive spillage of the substrate by foraging animals
2. Sufficiently durable to withstand weather conditions and animal use

Substrate

1. Similarity to the animal's natural foraging habits
2. Sufficient volume to insure that the animal's harvest rate increases with the abundance of food item in the patch
3. Sufficient volume so that the animal's GUD is greater than zero
4. Easily separated from unharvested food items by sieving or sorting

Food Items

1. Expense
2. Preferences of study animal
3. Uniform size
4. Resistance to degradation and fragmentation under the experimental conditions

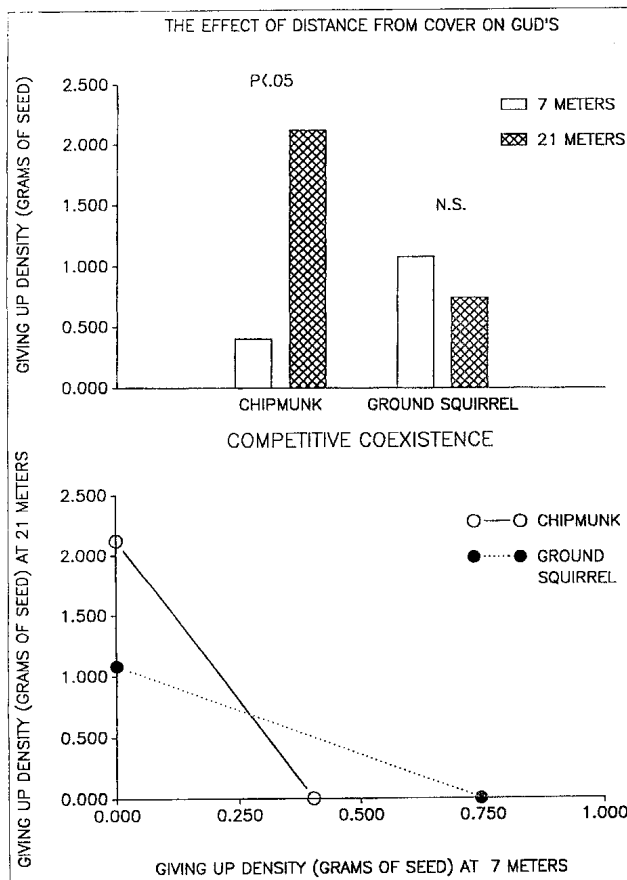


Figure 3. GUDs of chipmunk (*Tamias minimus*) and ground squirrel (*Spermophilus lateralis*) from montane meadows in Colorado (Smith unpublished data). The two axes represent different distances into the meadow from the forest's edge: 7 meters from cover and 21 meters from cover. The habitat heterogeneity of distance from cover promotes species coexistence. The chipmunk has the competitive advantage near cover (7 meters) and the ground squirrel has the advantage away from cover (21 meters).

remove the remaining debris. Weigh or measure the volume of the sorted food items to obtain that tray's GUD.

Statistical Analyses & Presentation of Results

Depending on the experimental design, GUD data are accessible to statis-

tical tests that range from the simple to the complex and from descriptive to inferential. Descriptive statistics such as the mean or mode of the data can be presented graphically, i.e. bar graphs showing mean GUDs as a function of specific experimental treatments. Such descriptive statistics may conclude the analysis, as some experiments provide

such dramatic results that students may discuss them confidently without establishing statistical significance. Paired data lend themselves to some of the simplest statistical tests. Such data arise when trays are placed in twos and the trays in a pair differ with respect to some experimental treatment such as substrate, habitat or food type. The effect of treatment can be determined either with a paired t-test or sign test.

When data are not paired or when there are a number of treatments, standard parametric statistics such as analysis of variance (ANOVA) may be applicable. For instance, trays might be paired with respect to food type with several pairs of trays distributed at different stations, and the experiment might be repeated over several days. In this case, the data could be analyzed as a paired t-test or, more appropriately, as a three-way randomized block ANOVA where the three factors are food type, station and day. Such a test will reveal the significant effects of each factor on GUD as well as the three interaction effects of food-type by station, food-type by day and day by station. When using parametric statistics we have found that a logarithmic transformation normally distributes the data. Useful non-parametric tests for comparing treatment means include the Wilcoxon's signed-ranks test, Friedman's method for randomized blocks or Kruskal-Wallis non-parametric ANOVA.

Data from food patches may include the presence or absence of feeding or some other type of frequency data. For such data we have used Chi-square goodness of fit tests or G-tests of heterogeneity (see Sokal & Rohlf 1981 for the application of the aforementioned statistical procedures).

In any experiment there will always be residual variation in GUD among replicate trays. Students should be encouraged to hypothesize about possible sources of this variation, for example: Was it cloudy one day but not the next? Was there the same amount of disturbance on all days? At all trays? Can differences be attributed to the size or sex of the foragers? An understanding of the possible sources of variation can lead to the design of additional experiments, as well as provide new variables for consideration. This is, by definition, the scientific method and it can lead students to think of science as a process instead of a collection of facts.

To broaden an experiment's context, we suggest discussing experimental results in terms of their relevance for

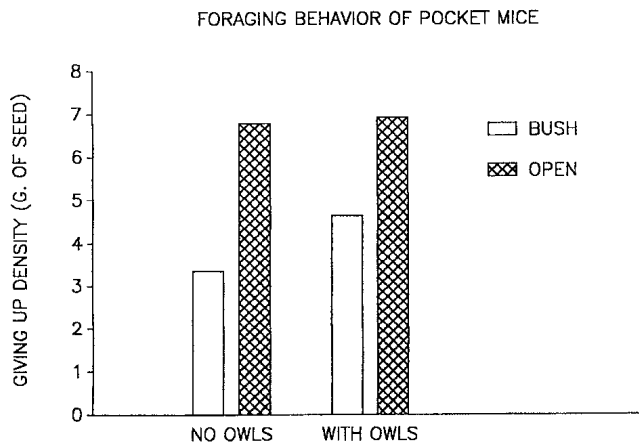


Figure 4. The effect of owls on the foraging behavior of the Arizona pocket mouse (*Perognathus amplus*). Experiments were conducted in a large aviary that was tailored to simulate a desert environment with a community of pocket mice. Experimental nights varied in terms of whether barn owls were present or absent from the aviary. In such a desert, there are two microhabitats: under the canopy of shrubs (BUSH) or in the open space between shrubs (OPEN). Shrub canopies provide protection from aerial predators such as owls. In response, the pocket mice always had a lower GUD in the bush microhabitat than in the open. In response to the presence of owls, the pocket mice demonstrated their increased perception of risk by increasing their GUDs in both microhabitats (Brown et al. 1988).

questions of species diversity and conservation. For example, if the students' results indicate a role for environmental heterogeneity in promoting species coexistence, then the students are only a step away from realizing that the elimination of habitat types might foretell species extinction. Students can also discuss the significance of such measurable phenomena as diet specialization, seasonal changes in food values or competitive abilities (why are owls predominantly out at night while hawks are predominantly out by day?) and why a food's appeal to an animal might be habitat-specific (what looks like a lot of forage to a game manager might not to a deer).

Some Suggested Projects

We have divided projects by area of ecological interest, although a well designed experiment and more advanced multifactorial statistics can be used to combine different questions into a single study.

Studies of Predation Risk

Predation risk can be measured on either a habitat or a patch scale. The easiest projects are those that examine the effect of habitat structure on perceived predation risk. Trays can be placed in pairs, one in an open area, another near some type of cover, such as a shrub or tree, park bench, etc. We have used this design with birds, desert rodents and montane ground squirrels. Different GUDs found between habitat types indicate greater or lesser predation risk. Manipulative experiments can follow, e.g. adding cover such as a large stick or rock pile to the open habitat or increasing predation risk by disturbing the foraging animals or using a facsimile of the predator. Figure 4 gives results for how owl predation influences the foraging behavior of a desert rodent, the Arizona pocket mouse: *Perognathus amplus* (Brown et al. 1988).

On a patch scale, we have mixed seeds into sifted cat litter and sand. The treatments were litter used by a cat and litter fresh from the bag. Seed

trays were placed out at night and the house mice in the area foraged in the trays. The mice in this study had a higher GUD in cat trays than in non-cat trays.

Other possibilities include: Measure GUDs before and after a scare by a predator (perhaps the experimenters) to examine recovery times; compare responses among species or among individuals of different age or sex.

Studies of Harvest Rates & Metabolic Costs

Does the color of the food item affect its harvest by a forager? Does the size of the food item affect its harvest? How does substrate type affect harvest rates? Do species of different sizes show the same preferences? How does the temperature of the patch (e.g. the weather) affect GUDs? What is the effect of hunger level on an animal's use of a food patch?

Studies of Missed Opportunity Costs

Do GUDs vary between breeding and non-breeding individuals; between those that are or are not territorial; between males, females or juveniles? How are GUDs affected by the addition of alternative feeding opportunities (for example, close to or far away from an area where students have lunch)?

Measuring Competition

The identity of the last species in a patch can either be assumed from the time of activity (e.g. nocturnal vs. diurnal) or discerned through the footprints on the surface of the dirt or sand. The GUD of the tray should be assigned to the last species that used the tray. Comparisons between the GUDs of different foragers or species in any of the above experiments will indicate which species is the superior competitor under the conditions in a given patch. Recall that the forager with the lowest GUD has an advantage because it can continue to use a patch after its competitors have quit. Coexistence may be promoted when each species has a distinct habitat or condition in which it is the superior competitor (refer to Figures 2 and 3).

Special Cautions & Considerations

Although we have used foraging trays successfully in many projects, there are some conditions in which they do not work. The first is rain. If

you are using sand or dirt in your trays, it must stay dry. It is virtually impossible to sift mud. Alternative substrates include gravel or wood fibers (the type used for packing in the Southwest). Unfortunately, these do not allow for species attribution, since no footprints are left.

Finding an appropriate food type may require numerous trials. If a food is perceived as very valuable or very easy to find then the GUD may be zero. If the food has little value or is impossible to detect then the animals may do no more than dabble in the food patches. However, the enthusiasm with which particular animals approach food patches provides insights into their foraging preferences and their abilities to negotiate particular foraging substrates.

Another problem arises when animals are not given enough time to make an assessment of the patches. We suggest that animals be allowed to experience the trays and food items at least a few days before the experiments begin. Prebaiting, the placement of additional food items around the trays, may encourage animals to forage in them sooner.

Other problems that might occur involve multiple species or individuals foraging in a tray. For example, seed trays placed out in the evening will be used by nocturnal mice, but if they are not collected in the morning, birds may also feed in them. To prevent this, the data must be collected before the birds begin feeding. When different organisms attempt to forage at the same time (and you are only interested in one of them), they can be

isolated by trying different substrates and/or food types. For example, we have kept the food in squirrel trays away from birds by burying it in sand or covering it with wood fibers.

A related problem is that of multiple individuals from the same species foraging in a single tray. This results in a bias of the data towards the most efficient individual, that is, the one with the lowest GUD. In interspecific comparisons this may strengthen the conclusions, because in effect you are comparing what the "best" of each species can do. To increase the independence of data points, place trays far enough apart to attract different individuals or sets of individuals.

Conclusions

An animal should continue harvesting the food from a patch until the benefits from its harvest rate no longer exceed its combined metabolic, predation and missed opportunity costs. As a result, the amount of food remaining in a patch following exploitation by an animal (its giving up density, GUD) can reveal its perception of its environment. The technique of using GUDs to measure patch use allows students to test hypotheses regarding how food, substrate, climate, predation risk and habitat influence animal behavior. The technique is general and can be applied across a variety of field situations (from backyards to mountain meadows), food types (millet seeds to cat food) and study animals (house sparrows to coyotes). The tight link between the theory of balancing costs

and benefits and the theory's implications for animal behavior encourage maximum student participation in formulating testable hypotheses and executing field experiments. In the process of conducting field experiments students acquire knowledge of their study animals' habitat preferences, food preferences, patch use behaviors and relative competitive abilities. This knowledge provides insights into the role of predators and habitat heterogeneity in species coexistence. All of this knowledge has relevance for the conservation, maintenance and restoration of biodiversity.

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