A Simulation of Optimal Foraging: The Nuts and Bolts Approach

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FOR THE PAST several years, ecology classes at the University of Wisconsin-Madison have used a mechanical model to introduce students to the branch of optimal foraging theory that focuses on the benefits and costs of feeding on assemblages of prey that have various feeding and handling characteristics. The success of this approach and its popularity with students has prompted this brief description. Additional details, including a copy of the exercise handout, are available from the author on request.

At least one other optimal foraging laboratory has been published (Charnov *et al*., 1976), but it is a pencil-and-paper exercise. In our version the prey are real entities that are caught by the students under the constraint of a time limit. Most students respond enthusiastically to this challenge. The exercise has the further advantage of giving students an opportunity to compare the success of various predators in different environments. One disadvantage is the rather high initial investment in equipment, but the materials will last forever; and if the laboratory is discontinued, the parts are readily reusable.

The Physical Model

Holling (1959, 1965) derived some of the fundamental equations of predation rate using data taken while a blindfolded individual searched a tabletop for sandpaper disks. Our exercise is an extension of this work. Our environment is a plywood sheet about .75m × 1m, but size is not critical. The sheet is studded with an assortment of protruding machine bolts, threads up, with a hex nut on each. We use 1/4-inch, 3/8-inch, and 7/16-inch diameter bolts to represent small, medium, and large prey. Blindfolded students search the board for prey; once the prey is discovered, the nut must be unscrewed. Removing the nut simulates the predator's handling of the prey. The model has no provision for pursuit of prey; thus, the best biological analogs are found in predation similar to that of bark or foliage gleaning birds that do search for and handle prey but that rarely have to pursue it. Handling time is adjustable by the number of turns required to remove the prey nut; we use a wooden spacer or a stack of washers to standardize this figure for each prey type.

Morphological specialization of predators is simulated by requiring the use of mechanic's tools for removal of the nuts. The "generalist" predator uses a set of three box-end wrenches of the appropriate sizes; this ensures approximately equal competence at handling all prey types. The other predator type is a "specialist" on medium-size nuts; s/he wields a correctly sized twelve-point socket wrench on a speeder handle. A speeder handle is simply a crank with a knob on one end and provision for attaching a socket at the other; it allows rapid turning of low torque nuts. The best size is 3/8-inch square drive. The speeder handle allows great proficiency with the medium prey, but the specialist must use a clumsy 8-or 10-inch adjustable "crescent" wrench to capture small or large prey. This limitation accords with the "jack-of-all-trades, ace-of-none" proposition that underlies most theorizing about animal adaptation. To continue the analogy to birds, birds with highly specialized bills (such as the Crossbills, whose mandibles overlap) are probably very efficient at harvesting certain types of food (coniferous tree seeds in the case of the Crossbills), but much less efficient at handling nonspeciality items than a bird with a more generalized bill would be. The relative success of these predators, which could be viewed as a competitive balance, shifts with changes in the distribution and abundance of prey. For simplicity, all our prey are the same height and diameter—extra width is provided for the smaller sizes by drilled dowel spacers that also serve to fix handling time—so that all sizes are equally likely to be encountered. (The simulation can be made more complex and the analysis more interesting if the prey are differentially conspicuous.)

The prey distribution on the boards may be varied in both overall density and proportional representation of

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the three prey types. A suggested set includes two moderate density (40-50 prey per square meter) board, one of which favors the specialist, one, the generalist. A third board should have the same relative abundance as the specialist-favoring board, but the density should be halved. Others can be added; the generalist can win due to a preponderance of smalls, of larges, or of a combination.

Operation

Four students make an ideal team; three are sufficient. One is the predator; one keeps time and records data; and the other one or two replace the nuts as they are harvested and hand the predator the correct tool for each item encountered. This last should be done in an impersonal manner, similar to the operating-room transfer of instruments from nurse to physician.

If hands are used for searching, prey are found too rapidly to allow the use of a small board. We hobble our searchers further by making them search with a 30-cm long by approximately 3mm-diameter wooden applicator stick, grasped at the top and held near the vertical. This slows the encounter rate very substantially, and prospective predators should practice for a few minutes to get the feel, as either extremely slow searching or violently fast searching both lower the success rate.

When a prey is encountered, the predator slides his/her hand down the stick to make contact. At this point the timekeeper, who has been recording search time since the start of the run, notes the time as the changeover to handling mode and records the prey type. The tool assistant hands the predator the correct tool. The predator may use his/her free hand to steady the nut, or to keep the wrench in alignment, but all turning must be done using the wrench. It must be further stipulated that the adjustable wrench must move more or less parallel to the board; some unfair advantage can be gained by twirling it vertically.

When the nut falls free, the timekeeper returns to search time, the predator's stick is returned, and the nut is replaced. (Replacing the nuts is also an option for mathematical simplicity, which may be abandoned in favor of no renewal, or a more biologically inspired renewal rate dependent on population size.) We require predators to take all prey encountered, even though this is sometimes galling to the specialists. This is done because we need handling-time data for all prey types. This constraint also could be lifted once those data are in hand, allowing predators to try to optimize their intake based on progressive sampling, as in the Charnov, *et al*. model. We find that four minutes is a good run length; then team members can trade roles or boards.

The Theoretical Model and Data Analysis

The data obtained can be manipulated in several ways. We follow Schoener's (1969, 1971) formulations (1) to predict the optimal diet for a particular predator in a particular environment, and (2) to construct a graph (the e/t curve) to examine the time course of energy gain as items are progressively added to the diet. The analysis uses energy gain per time (e/t) as a measure of foraging efficiency, and the optimal diet is that which maximizes this quantity. The computation of e/t is a simple algebraic balancing of cost terms associated with finding and harvesting prey and gain terms representing food intake.

The relevant variables are summarized in table 1. The two cost terms and the calorie content of the prey must be supplied as givens, and these values should be chosen after some preliminary testing with the system. Using the notation of table 1, Schoener's equation for the mean energy per time for a particular diet can be written as follows:

$$\text{mean } e/t = \frac{-e_s + \sum_i (p_i(e_{fi} - e_{hi}))}{t_s + \sum_i (p_i(t_{hi}))}.$$

TABLE 1. Parameters of the Model

Symbol	*Units*	*Definition*	*How obtained*	*Dependent on*
t_s	sec	mean search time between items	measured	board type: prey density
c_s	cal/sec	cost of searching	given	(predator type)*
e_s	cal	energy of search	$c_s \cdot t_s$	prey density, predator type
t_{hi}	sec	mean handling time for prey type i	measured	prey type, predator type
c_{hi}	cal/sec	cost of handling item i	given	prey type, (predator type)*
e_{hi}	cal	energy of handling item i	$c_{hi} \cdot t_{hi}$	prey type, predator type
e_{fi}	cal	food energy content of item i	given	prey type
P_i	ratio	proportion of items which are type i	counted	board type: prey composition

*These values will usually be the same for both predator types to facilitate comparisons.

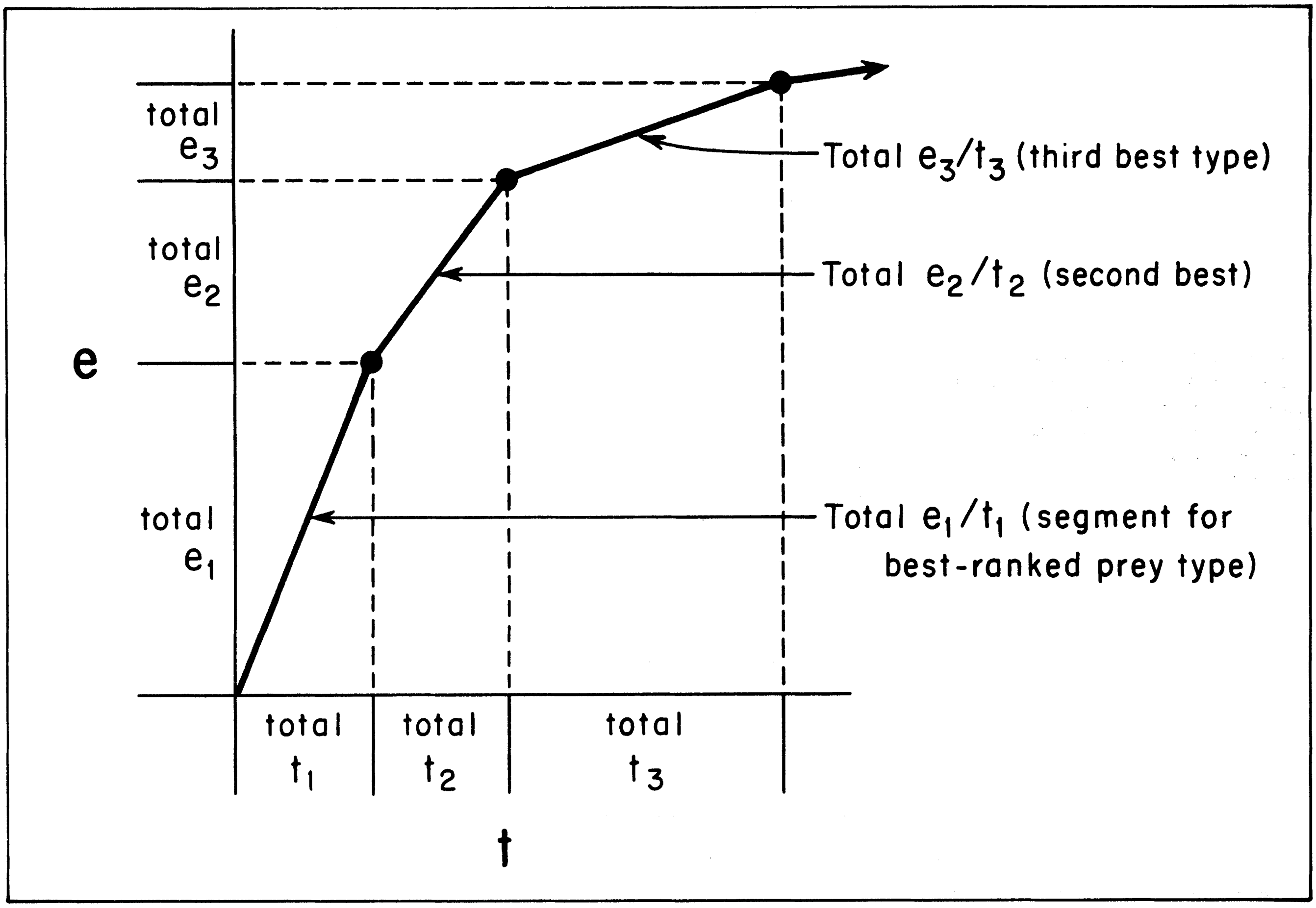

FIGURE 1. The "e/t" curve, which shows how energy gain per unit time decreases as less suitable prey types are sequentially included in the diet. The slopes of the segments associated with the different types equal the efficiencies with which they can be harvested.

For details of the derivation, see Schoener or our laboratory handout (supplied on request). To use the equation to find the optimal diet, one must first rank the three prey types by the ratios of their net caloric reward (calorie content minus handling energy) to the handling time required to secure that reward. The best is termed prey type 1, the next best 2, the worst 3. The equation is evaluated for the three possibly optimal combinations: prey type 1 alone, 1 plus 2, and 1 plus 2 plus 3. The combination giving the highest e/t is optimal. The optimal diet depends heavily on the prey environment; for instance, a diet of all medium nuts will not be optimal for the specialist unless mediums are rather common.

The e/t curve, in contrast to the optimal diet computation, considers the total prey available to a predator; this may be the total available in the home range, for instance, or the total available in a day's foraging. For the lab, it may be computed as the number of prey on the board or the average number encountered during a run. Because the curves are used solely for comparisons, it is important to base each curve on the same parameter. Search can also be ignored if the curves are only to be used to compare specialist and generalist, and search *is* ignored in the following outline. One calculates the net energy gain (total food energy - total handling energy) the predator could realize by taking all the best ranked prey available; the

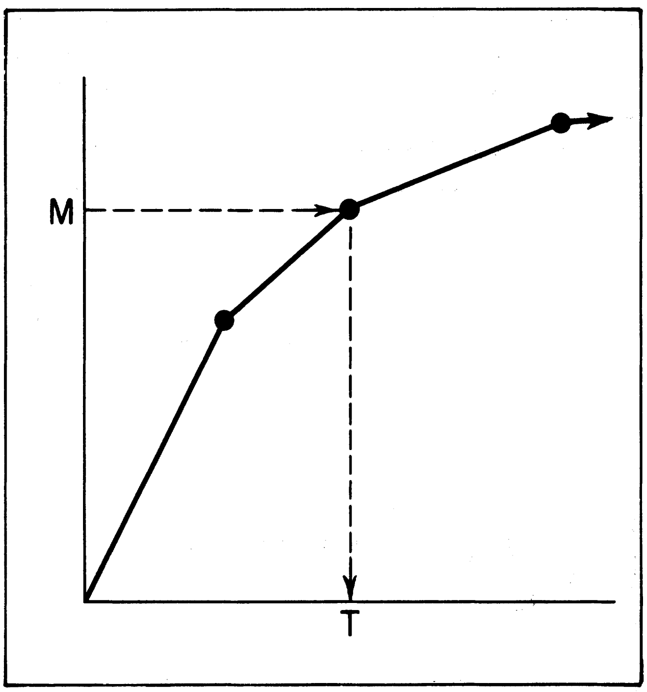

FIGURE 2. Every point along the e/t curve determines the combination of prey items that will provide a given amount of net energy gain in the shortest time, *i.e.*, the optimal diet. In this case, a predator with a metabolic requirement of M calories will meet that requirement in minimum foraging time T by taking all of the best and second-best prey which it encounters, but ignoring the third-best.

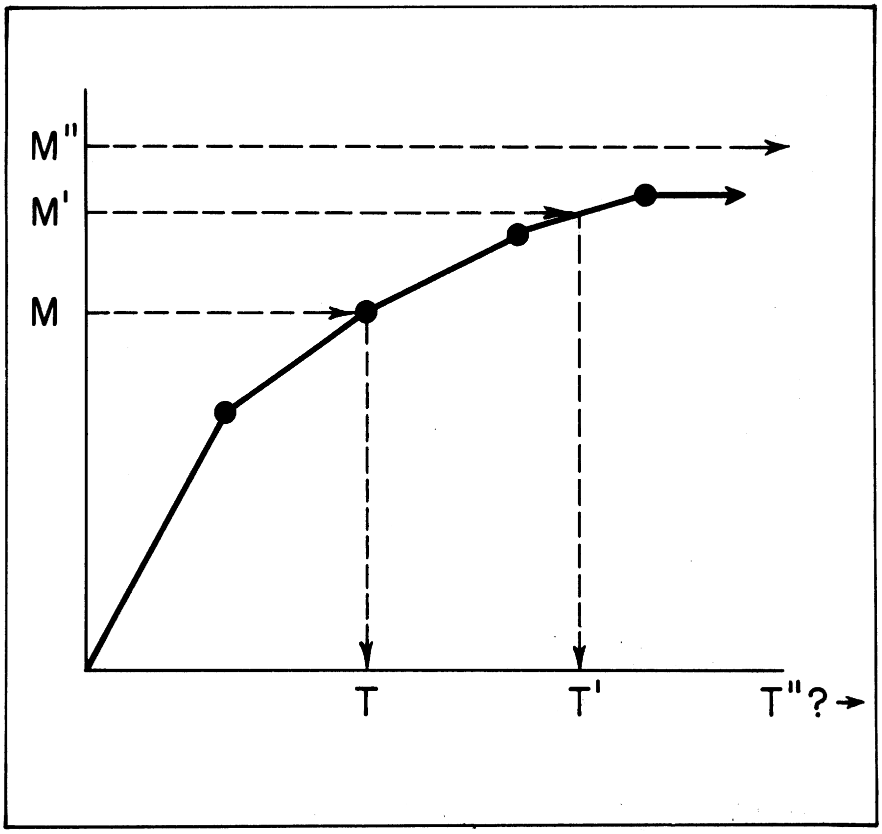

FIGURE 3. A moderate increase in energy requirement (M to M') may cause a large increase in required foraging time (T to T'). Predators with very high requirements (M") may be unable to survive on a given food distribution.

total handling time required is also computed. These two values specify a point in a graph of energy *vs.* time (fig. 1). A line segment drawn from the origin to this point gives the first section of the e/t curve: its slope, by definition, *is* e_1/th_1, and its length is proportional to the items available. The points along this line are the possible combinations of energy gain and time expenditure that the predator can realize by taking only the best items. If the predator begins taking item 2, energy no longer comes in as quickly as it did while item 1 was being fed upon; the

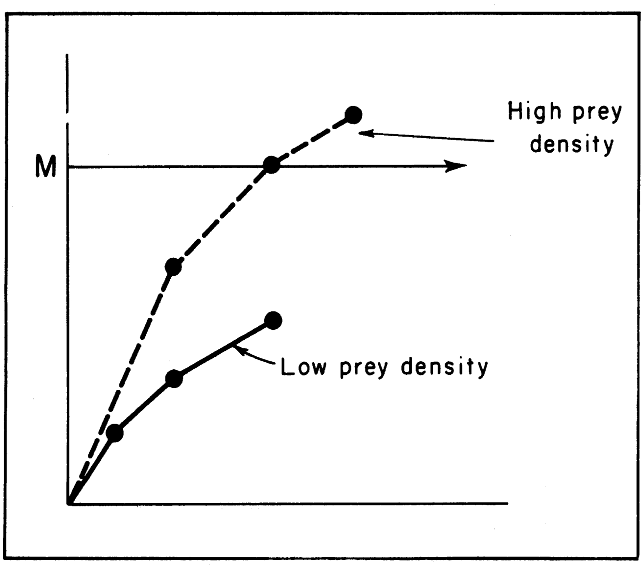

FIGURE 4. As prey become more common, the line segments associated with them become longer, but the slopes remain constant. At high prey density an optimally foraging predator will specialize on the best items only.

total energy obtainable, and the time required to eat all the second ranked items are added to the totals from item 1. This effectively chains a second line segment, with a smaller slope, onto the first segment. The third ranked item yields a third segment to be chained onto the first two, and the e/t curve begins to show its essential characteristic, a continually decreasing slope, as more items are added. The usefulness of the curve is this: for any fixed amount of time allowed for foraging, the curve tells what combination of items will give the most energy, and it tells what that energy is. Similarly, if a predator has some minimum energy requirement, the curve gives the prey combination that will meet that requirement in minimum time.

Suppose the daily metabolic requirement of the predator is M calories. The curve indicates the most efficient combination of items. Dropping a perpendicular to the time axis shows how long (T) it would take to harvest this requirement (fig. 2). A predator with a higher metabolic requirement M', working on the same prey population, would have to take a wider variety of prey, and take more time. This might well be suboptimal foraging. A very high requirement M" may be impossible to meet under these conditions (fig. 3). However, an overall increase in prey density, which increases the lengths of the segments without changing their slopes, can allow survival of species with high M (fig. 4).

Consider generalists and specialists again. Specialists should do well (high slope) on their best prey species but lose efficiency on non-preferred prey; this would give a bowed e/t curve, in contrast to the flatter curve of a gen-

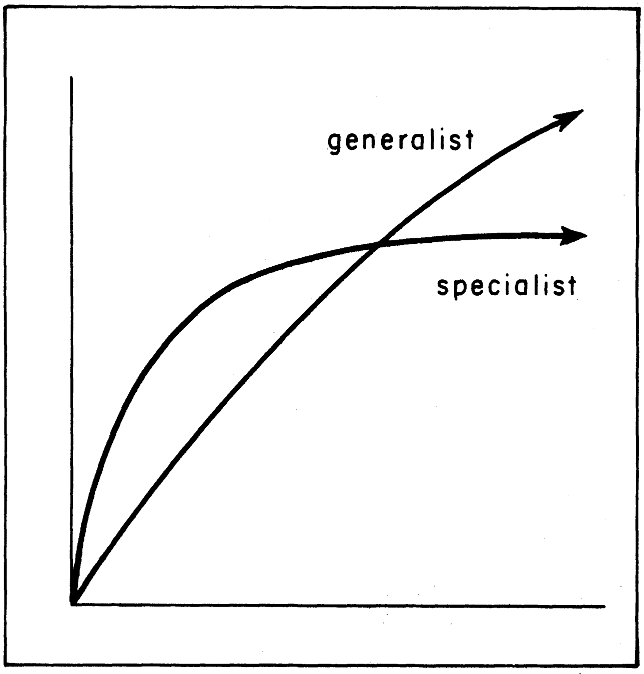

FIGURE 5. The formal relationship between generalist and specialist foragers. The curves are smoothed, representing a situation with many prey types. By assigning different tools, representing different foraging abilities, to different students, the laboratory exercise compares generalist and specialist feeders in a variety of prey environments.

eralist (fig. 5). The intersection point shows where the two species are competitively equal. It is evident that the specialist will be favored when its preferred prey is abundant, even if the other prey are also abundant; but that it may do poorly when this prey is scarce. The generalist will fare better when prey are scarce, especially the specialist's favorite.

As previously mentioned, these e/t curves do not incorporate search, although they are suitable for comparing feeding specialists and generalists whose search costs are the same. The inclusion of search does not change the *shape* of the e/t curve, but shifts its position relative to the axes. The curve moves to the right a distance equal to the total time required to encounter all the items available, and it moves downward a distance equal to the total calories expended in that search. Thus searching the habitat but taking no prey will result in time expenditure and a caloric deficit.

Conclusion

We have found that the boards provide a comparatively stimulating animal-related lab exercise well suited to seasons when field work is difficult. They also generate a data set that is complicated but flexible enough to be analyzed at several levels. The simulations seem to make the equations more real to some of the students who distrust abstraction. I also suspect that what understanding of optimal foraging they provide is less transitory than that provided by lecture alone.

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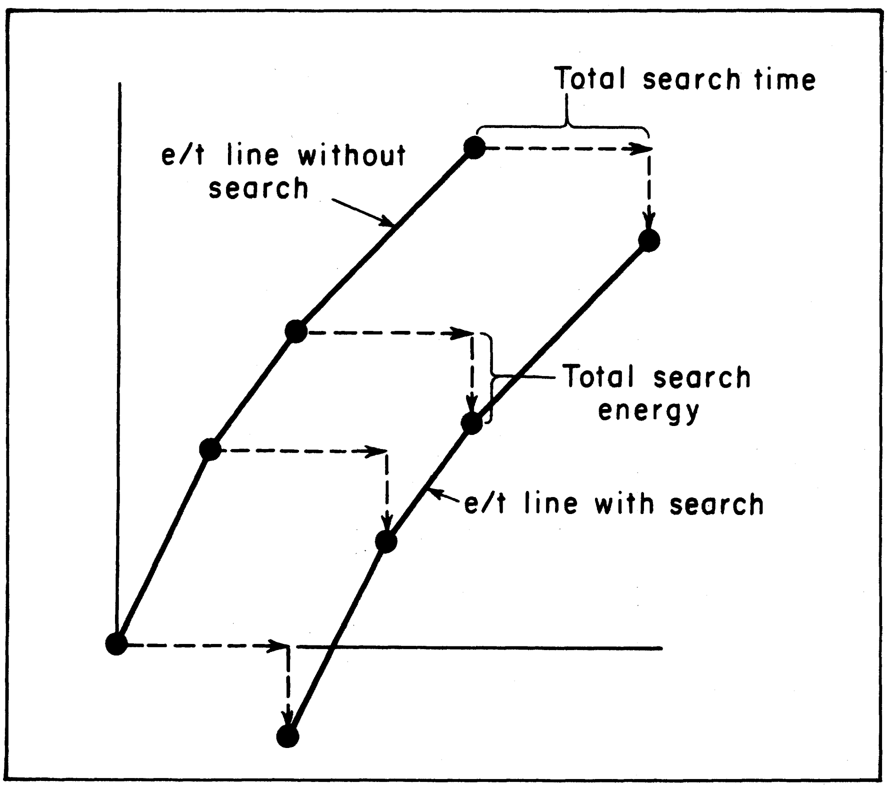

FIGURE 6. Incorporation of search costs; the e/t curve is constant in shape but moves relative to the coordinate axes.

FIGURE 7. Students using the "Nuts-and-Bolts" approach.

References

CHARNOV, E.L., ORIANS, G.H., FOWLER, C., and PEARSON, N. 1977. The optimal foraging game. In Crowder, L.B. (ed.), *Ecological lab experiences: An ideas forum*. Michigan State University Department of Zoology.

EMLEN, J.M. 1966. The role of time and energy in food preference. *Amer. Nat.* 100:611.

______. 1973. *Ecology: An evolutionary approach*. Reading, Massachusetts: Addison-Wesley.

HOLLING, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385.

______. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Ent. Soc. Canada* 45:5.

PYKE, G.H., PULLIAM, H.R., and CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 52:137.

SCHOENER, T.W. 1969. Optimal size and specialization in constant and fluctuating environments: An energy-time approach. *Brookhaven Symp. Biol.* 22:103.

______. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. and Syst.* 2:369.

Plant Growth

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razor blade will greatly reduce, but not abolish the geotropic response in corn. If only the cap is removed (as opposed to the cap and the root meristem that should remain intact), the growth rate will remain the same for both the capped and uncapped roots, but the degree of curvature will be reduced. Growth rate can easily be measured with a ruler after a 24-hour period (measure mm growth/24 hours). The angle of curvature is measured with a protractor as shown in figure 4.

The experiments described in this article can be used in studies from high school to graduate school. At less advanced levels, the data should be more observational, but each experiment does lend itself to a quantitative approach to plant growth. Each experiment can also be adapted to further study on the more advanced level. For example, auxin can be exogenously applied to various part of corn or oat coleoptiles in the phototropism study. Such treatments may either enhance or negate the natural response, depending on the site to which the hormone is applied.

In all of these experiments, however, it should be stressed that before the plant can respond to the environment, it must be able to sense in some manner that a change in environmental conditions has occurred. The mechanisms responsible for perception by plants are the subjects of active current research.

References

BIDWELL, R.G.S. 1979. *Plant physiology*. 2nd edition. New York: MacMillan Publishing Company, Inc.

HOLMES, N.G., and SMITH H. 1977. The function of phytochrome in the natural environment-IV. Light quality and plant development. *Photochemistry and Photobiology* 25:551.

MOORE, T.C. 1979. *Biochemistry and physiology of plant hormones*. New York: Springer-Verlag.

NOGGLE, G.R., and FRITZ, G.J. 1976. *Introductory plant physiology*. Englewood Cliffs: Prentice-Hall, Inc.

WILKINS, M.B. 1975. The role of the root cap in plant geotropism. *Current Advances in Plant Science* 13:317.