Chapter 5

"Optimal" Organism Design and Costs for Not Being Perfect

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Introduction

The two exercises described in this chapter are taught to second-semester freshman majors in “Biology of Organisms,” part of a five-semester Bachelor of Science core sequence, but they easily can be modified for a general course for majors or non-majors. The goal is to teach “how to do science.” The approach is to develop hypotheses and predictions in lectures, and to test them in the laboratory. Analysis is with comparisons of averages, frequency distributions, and graphical visualization. After doing these by hand, students use computers to speed analysis in the lab.

Exercise 1 involves calculating and graphing average volume and average sugar rates of ingestion through butterfly proboscides and pipets. Students then design a choice experiment with butterflies and analyze results with a binomial test. The lab takes 3 hours, but it cannot be completed in time without computers. It can be finished in time without computers by only doing the feeding rate measurements. The sugar ingestion rates are used in Exercise 2.

In Exercise 2 students compare predicted with observed shapes for cylindrical containers and calculate costs for non-optimal shapes. The ideas are then applied to the results of butterfly sugar ingestion rates. Predictions in lectures and the Student Outline use calculus, but the ideas can be developed with a slight modification in procedure without calculus (see Notes for the Instructor, Exercise 2). Exercise 2 takes 2 hours, and computers are not important in timing. It is given at the end of the course to emphasize how organisms must integrate functions to solve multiple problems.

Times for both labs assume students are prepared. To enhance this, they are not allowed to bring student outlines to the lab. They must bring their notes on what they have read. Each lab starts by answering all student's questions (10–15 minutes) followed by a short quiz (10–15 minutes) (see Notes for the Instructor). Students are then instructed to begin work. There is no “lecture” in the lab repeating material students are already familiar with, although introductory material can be adapted from the Introduction in the Notes for the Instructor (Exercise 1) and associated references. The last 45–60 minutes of each lab are devoted to analysis. Students write reports following a journal format, and the Student Outlines contain questions printed in italics that they must answer in the reports (see Notes for the Instructor).

Student Outline

Exercise 1:
Fast Food versus Haute Cuisine: "Optimal" Ingestion of Fluids Through Tubes

Introduction

Some biologists hypothesize animals should feed so they achieve a maximum possible rate of net energy gain while they are foraging because this could mean they may be more likely to survive and reproduce (Stephens and Krebs, 1986). If this is true, and if there is some predictability to the nature of food, then we can hypothesize that the apparatus used to ingest food may have been designed through natural selection to achieve this goal. We will test for this idea in this laboratory using two simple systems where it is possible to: (1) quantify gains of energy/time during ingestion, and (2) ask whether an animal selects the food yielding the highest rate of net energy gain while it is foraging. The "systems" are the Painted Lady butterfly (*Vanessa cardui*), which normally feeds by sucking nectar (sugar water) from flowers through its tubular proboscis, and humans sucking fluid through a pipet (a fancy substitute for a soda straw).

Fluid flow (volume/time) through tubes is described by the Poiseuille equation. This is discussed in your textbook (Schmidt-Nielsen, 1990) in the chapter on circulation where similar

$$Flow = \frac{\Delta P \pi r^4}{8 l \eta}$$

problems for flow are involved:

where: ΔP = pressure difference across the length of a tube,
r = radius of tube,
l = length of tube, and
η = fluid viscosity.

Rate of volume flow decreases as viscosity increases, and viscosity increases as concentration increases. Energy content also increases with concentration for sugar solutions (each mg of sucrose has an energy value of 16.48 joules when completely oxidized to carbon dioxide and water). How do these variables interact to influence rate of *energy* ingestion? At low sugar concentrations viscosity is low, so rate of volume ingestion should be high, but energy content is low. At high concentrations energy content is high, but so is viscosity, so rate of energy gain may be low. Perhaps the rate of energy gain is highest at an intermediate sugar concentration.

Butterfly Ingestion

Mixing Solutions

We will use sucrose solutions of 8.75%, 17.5%, 35%, 50%, and 80%. Fifty percent is 50 *grams* of sucrose in a total *solution* volume of 100 ml. The 80% solution will already be prepared for you because it takes a long time to dissolve that much sucrose. You will not need large volumes, so make up the solutions of 35% and 50% sucrose to a volume of 100 ml using screw-top plastic bottles. Weigh the sucrose on the beam balance, and transfer it to the bottles using the powder funnels.

Pure sucrose has a specific gravity of 1.588 g/ml. Use this to calculate the volume of water to add for both a 35% and 50% solution so total solution volumes will be 100 ml. Do this by dividing the weights of sucrose (35 and 50 g) by 1.588 g/ml. What are the units when you divide grams by g/ml? These are the volumes the sucrose will occupy in the solutions. Subtract them from 100 to obtain the volumes of water to add to obtain final solution volumes of 100 ml. Use the graduate cylinder to add the water to the bottles. Shake until all the sugar is dissolved. Obtain the 17.5% and 8.75% solutions by serial 1:1 dilutions using 15 ml of 35% and 10 ml of 17.5% sucrose.

Calculating Solution Specific Gravities

You will eventually be weighing butterflies to find out what volumes they ingested. To find volumes you need to be able to convert a change in mass due to the food ingested to the volume ingested. This is done by using the specific gravities for each of the solutions you will feed to the butterflies.

Calculate the specific gravity for each of the solutions, including the 80% solution. This is relatively simple to do because you know the masses of the sugar and you know that 1.0 ml of water has a mass of 1.0 g, so all you have to do is add to find the total masses of your solutions, and then divide them by 100 to know g/ml for each solution. Because this takes a little time, you should do all the necessary calculations of volumes of water and specific gravities for each solution before you come to the lab. When you get to the lab you can compare your results with others in your group to make sure everyone knows the correct values. If you do not understand how to calculate specific gravities, be sure to ask about it at the beginning of the lab because your quiz will have a problem where you will have to do the calculations.

Feeding Butterflies

Each group will have some butterflies to work with. Each group should try to keep 1–2 butterflies unfed for the choice experiment described later. The butterflies will be in a container, and you will have an empty container in which to place them after they have been fed to satiation. Be careful about how you handle them as they are easily damaged. They should be held by their wings. Grasp them with your index and middle fingers when they hold their wings closed. If they escape they will most likely fly to the windows where they are easy to catch.

The instructor will review how to use the analytical balance which can be used to weigh the butterflies to 0.0001 g. Place a butterfly in a cup made from two 50-ml plastic beakers taped to each other. Weigh the butterfly in the cup on an analytical balance before and after each feeding and following any excretion that will change weight. You will find that the butterflies may excrete a reddish fluid the first few times you pick them up. You do not need to weigh the cup separately as long as you use the same cup for weighing each time. You will find that the butterfly may jump up and down in the cup, and this will make it difficult to obtain an accurate weight on the analytical balance. You need to wait until it is quiet for a few seconds, and the balance weight is steady.

After weighing, hold the butterfly carefully by the wings and place its legs in a small dish containing a sugar solution. This is easiest to do if you hold the butterfly close to the table top until it extends its walking legs so they touch the table. You can then "walk" it into the sugar solution. The chemoreceptors on the tarsi (last leg segment) should elicit proboscis uncoiling and extension. If not, you can use a small probe to uncoil the proboscis and place its tip in the sugar water.

Time ingestion with a stopwatch from the moment the proboscis contacts the fluid until contact is broken by you or the butterfly. Feeding should be faster at lower concentrations, so allow a butterfly to feed for 1 or 2 minutes before reweighing, but you can allow 5 or 6 minutes at the highest concentration. Re-weigh the butterfly in its cup. Repeat the method to obtain one set of measurements for each concentration. Record the weights following each feeding, and the times for those feedings, in separate columns on a data sheet.

Calculating Volume Ingestion Rates

Use the information on fluid specific gravities to calculate the volumes ingested by your butterflies. We wish to calculate the ingested volumes in nanoliters. Say the mass changes by 0.000X g. Dividing by specific gravity *of the solution consumed* (g/ml) will give ml, and moving the decimal point three places to the right will give you µl. This will give you a number where you can again shift the decimal point three places to the right so you have nanoliters. Start by using one of the weight changes you have measured and calculate the volume consumed in nanoliters. Then ask the lab instructor to check your figures before doing the other calculations from your weight change measurements.

Once you have all your nanoliter intakes, divide each by their corresponding seconds spent ingesting so your volume rates will be in units of nanoliters/second. Report your volume rate data to the lab instructor who will compile a data sheet for everyone to use to calculate averages and 95% confidence intervals based on the combined data for the class.

Calculating Sugar Rates of Ingestion

We wish to know the sugar rates of ingestion in µg/second. You know nanoliters/second, so you want to know µg of sucrose/nanoliter of solution so you can multiply to obtain µg of sugar/second. Each ml of solution contains the percent sucrose as grams divided by 100; for example, the 35% sucrose contains 0.35 g of sucrose per ml of solution. Converting grams to mg and ml to µl both involve dividing by 1,000, so a 35% solution contains 0.35 mg per µl. Converting mg to µg and µl to nanoliters also both involve dividing by 1,000, so 35% sucrose also contains 0.35 µg of sucrose per nanoliter. Report your sugar ingestion rate data to the lab instructor who will compile a data sheet for everyone to use to calculate averages and 95% confidence intervals for each concentration based on the combined data for the class.

Making Graphs

Construct two graphs: (1) average volume (nanoliters/second), and (2) average sucrose (µg/second) ingestion rates, each showing plus and minus 95% confidence intervals for the averages, and each as a function of sugar concentration. Use the combined data from the entire class. Use Statview to calculate the averages and to calculate a value for "t" 95% (the width of the confidence interval). After you have an average and a "t" 95% value for each concentration, set up three columns in Statview: one for percent sucrose (assign *X*), one for average rate (assign *Y*), and the third for the "t" 95% values for each concentration. Then make a scattergraph and click on the small box in the upper left part of the screen with a dot and bar. This will give you a dialog box where you can pick the column containing the error measurements ("t" 95%). In this way you will produce graphs with each mean and its associated confidence interval. You can use this method to construct both the graph for volume rates of intake and the graph for sugar rates of intake.

Is there an “optimal” concentration for a maximum rate of sugar ingestion? Why? (Consider the slopes for volume rate and for sugar amount as a function of concentration.) Make an extra copy of the graph of average µg/second versus percent sucrose to use in a future lab.

Pipetting by Humans

You will find that a butterfly will stop feeding after it has consumed about 30–40 µl. But if feeding is influenced by tubes and fluid characteristics, we should be able to model this system with pipets. Chemists will tell you never to pipet by mouth to avoid any accidental ingestion of the fluid. We ignore this caution here because the fluid is a food.

Use the same sucrose solutions. Pour 10–15 ml into a 50-ml plastic beaker. One individual should time uptake to the volume mark on the pipet with a stopwatch while the other pipets *as fast as possible*. The pipettor should begin when the timer says “go” (when they start the stopwatch), and they should stop when the timer says “stop” (when the volume mark is reached). With this system you can collect measurements in a short time. Each group should measure seconds to ingest each concentration five times.

Volume rates in ml/second are very easy to calculate because they are the fixed volume pipetted divided by the seconds to get to that volume. Sugar rates in g/second also are easy because you know each ml contains the percent sucrose in grams as a fraction.

Enter the data from your group in Statview to calculate averages and 95% confidence intervals. Again, plot two graphs: (1) average volume (ml/second), and (2) average sugar (g/second) ingestion rates plus and minus 95% confidence intervals as a function of sucrose concentration. Use the same methods with the computer as you did for the butterfly data.

How do your results compare with those for the butterflies? Is the “optimal” concentration for either sharply defined, that is, are the functions narrow and peaked, or are they broad and flat (are adjacent average values statistically different based on 95% confidence intervals)? How might the shape of a function influence the way you interpret what butterflies or humans should do? Be sure to include the figures and answer the questions in your lab report.

Choices by Butterflies

Even though there could be a well defined maximum for rate of sugar ingestion at a particular sucrose concentration, this is no guarantee that butterflies would or should prefer that food to others. In fact, it can be hypothesized that a butterfly perhaps should ingest a more concentrated fluid (“haute cuisine”) because it would ingest more total energy in a meal with that food even though it takes longer to eat than the “fast food.” What is more important to butterflies, saving time while they eat, or getting more energy? We can try to find out.

General Methods

We will eventually test for the preferences of unfed butterflies by giving them a choice between two foods at the same time. Use your “optimal” concentration that you have found for the maximum rate of sugar ingestion and the 80% sucrose concentration. You wish to place the legs on opposite sides in each of these at the same time to see which one the butterfly will select with its proboscis. Use small dishes made by cutting the bottom out of 50-ml plastic beakers. Make the edges very small so it will be easy to “walk” the butterfly into both at the same time. It is important to try to stimulate legs on both sides at about the same time because if one side is stimulated first, the butterfly may respond to that side without having information about the other side. You may want to practice a bit and/or ignore some trials when both sides are not stimulated by the time the proboscis uncoils (it usually takes several seconds for the proboscis to uncoil). Try to keep the legs separated as much as you can so the proboscis has to clearly move to one side or the other to indicate the preference.

Testing for Side Bias

Before doing the experiment, it is important to know whether the butterfly has a bias toward one side. You can test for this by placing its legs in two containers with the same concentration. Use the "optimal" concentration that you have defined from your measurements. Do this 10 times and dip the legs in water between each trial. Use hungry butterflies, and *do not allow them to feed*. Withdraw the butterfly just before its proboscis contacts a fluid, but after it has probed far enough to indicate its preference.

Choice Experiment

After your side preference trials you will know the fraction of probes the butterfly makes to each side. For your concentration preference trials place the most concentrated fluid in the *least* preferred location. If there is no side bias, use a coin toss to position the two concentrations. Conduct 10 trials for concentration preference using the same methods (no feeding, wash legs between trials).

Analysis

How can we decide whether they prefer a concentration? From the side preference trials we have the *expected* proportion of responses to a side without any difference in concentration. We might predict this to be about 50% to a side, but it does not have to be exactly 50%. Because there are only two possible outcomes for each trial (probe to the left, or probe to the right), the experiment is similar to tossing a coin and asking whether it comes up heads or tails. If a coin is not biased, we expect 50% heads and 50% tails, but it is possible to obtain several heads or tails in a row, that is, there will be variation in the proportion of heads or tails, just as there is likely to be variation in the responses of your butterflies.

We can calculate the probability of obtaining an observed proportion compared with an

$$P_{(x)} = \left(\frac{n}{x}\right) (P)^{x} (1 - P)^{n - x}$$

expected proportion using the binomial (two event) expansion. Use the following general formula:

where: n = total number of trials (this is 10 for the experiments),
x = number to one side,
P = fraction to that side expected (see below),
n/x = $[(n)(n - 1)(n - 2)$ .... x times$] \div X!$
and ".....x times" means you continue until you have multiplied x numbers.

Calculate the probability that your butterfly responded significantly differently from an expected 50% to a side with the same concentration on both legs by using 0.5 for P. For example, if the butterfly probed to the left 3 times out of 10,

$$P_{(3)} = \frac{(10)(9)(8)}{(3)(2)}(0.5)^3(0.5)^7 = 0.12,$$

so we would conclude this is not significantly different from 50% (because $P > 0.05$). Practice and verify the use of this formula before you come to lab by tossing a coin 10 times, and calculate the probability of heads or tails.

To decide about the experiment, use as your expected proportions for P the fraction to a side in the trials where the concentration was the same for both sides. Thus, if the butterfly probed 3 times out of 10 to the left when concentration was the same, use $(0.3)^x$ and use the number to that side during a concentration difference for x. For example, say the butterfly probed 7 times to the left in 10 trials with a concentration difference and 3 out of 10 without a concentration difference, then,

$$P_{(7)} = \frac{(10)(9)(8)(7)(6)(5)(4)}{(7)(6)(5)(4)(3)(2)}(0.3)^7(0.7)^3 = 0.009,$$

or significantly different ($P < 0.05$) from the expected proportion of 0.3.

Calculate your probabilities and show the step-by-step calculations in your lab report. *How do you interpret the results (for your lab report Discussion section)? What is an “optimal” concentration for butterflies based on your results? Why? (Think about time and energy.) Some biologists think that plants should have evolved to produce nectar to attract butterflies so the plants can be ensured of being visited and pollinated. What concentration would you predict for this based on your results? The average sugar concentration for nectars from plants pollinated by butterflies is about 35% sucrose, and it ranges from 10% to 65% sucrose. How do you interpret concentrations produced by plants based on your measurements and experiments?*

Exercise 2:
Solving Multiple Problems: “Optimal” Design and Costs for Not Being Perfect

Introduction

Optimal means “the best.” In biology it may mean being “fitter” than others, but fitness can operate over relatively long time scales, so biologists interested in design by natural selection often examine short-term functions (such as feeding or mating) and make assumptions about how these influence longer-term reproduction and survival.

The process used to investigate structures and functions works best when it is possible to make an easily tested prediction about what may be “best.” Maximum-minimum calculus and analytic geometry provide tools for making predictions in some cases. They also can be useful to understand why there may be variation in what should be optimal. Your task in this lab is to examine a problem in the optimal design of containers using a little calculus and analytic geometry, and to use what you find to try to interpret why there may be so much variation in what should not vary both for containers and animals.

Some ideas about how natural selection may produce design in biology come from economics. The survival of a business depends on profits (net gains of money) which are influenced by expenditures (costs) for manufacturing and marketing. When there is a way to minimize expenditures, we would expect those in businesses to discover this so they can be more competitive and survive.

Cylindrical containers (cans or jars) are used by a large number of businesses to market their products. The containers must hold a particular volume of product. Costs might be minimized if there is an optimal shape for a cylindrical container, or one that minimized the amount of material needed to make it so it holds a particular volume. You may recall that we discussed this problem at the beginning of the course in lectures as an example of the ways we would be studying organisms. We return to it now to summarize and focus on some of the major approaches we have been using to understand adaptations.

Calculating a Prediction

Draw a picture of a cylinder with a radius, r, and a height, h, and write two equations, one for the surface area of the cylinder, and the other for the volume. If you do not remember, the area of a circle is πr^2, and the circumference of a circle is $2\pi r$. If you have difficulty with this, you can consult your notes from the beginning of the course where we developed the equations for this problem.

Using the equation for volume, solve for h, and substitute the solution for h into the equation for surface area. You should now have an equation for surface area that contains only volume and radius as variables. You wish to know if there is a minimum value for surface area as radius varies considering volume to be constant, so volume will be treated as a constant. Take the appropriate derivatives of surface area with respect to radius to decide if there is a minimum. If there is a minimum, solve for the value of radius at the minimum where the slope is zero. To remove radicals from this, express the answer as r^3. You can do this if you go back to the equation for volume you solved for h and divide both sides by r. You should produce a result containing r^3. Now take your value for r^3 at the minimum and substitute it into the equation for h/r. Simplify this and you will have a prediction for how a cylindrical container should be designed so the least amount of material is used to hold a particular volume of product. Show your step-by-step calculations in your report.

Testing the Prediction

We have collected a variety of cylindrical containers for you to measure to test this prediction about optimal design. The containers were obtained at local supermarkets and originally contained a variety of different kinds of products. Make the appropriate measurements to produce a frequency distribution bar graph for different values of h/r for all the containers. Two groups can share the same collection of containers; pass them one at a time after you make the measurements.

It is possible that a number of different products may be packaged in the same type of container, so perhaps including many of the same container type would distort the frequency distribution. For example, a variety of different products may be packaged in the same type of container when they have the same net weight. A way to correct for this is to construct a frequency distribution for h/r for all *unique* containers, that is, do not include containers with the same values for both h and r more than once. A quick way to do this is to use "Sort" under "Tools" in Statview. If you sort either height or radius in either ascending or descending values you can easily spot more than one measure of the same height to check whether radius is also the same. Do this, remove all duplicates (same height and radius), and compare the two frequency distributions.

How are your data for unique containers distributed with respect to your prediction? Is the distribution symmetrical, that is, are there about the same number of h/r values above and below the predicted optimum? How about above and below the average for h/r? Are the average, median and mode for h/r at the same category interval on the distribution?

Based on the range of values for *h/r*, draw a conclusion about the importance of optimal design for this problem in the Discussion section of your report. Suggest some hypotheses for why you think there may be so much variation in *h/r*, and why your data might show a particular type of distribution.

Assessing Variation in Cost

Perhaps some of your hypotheses involve multiple functions for container design. A container could have a variety of functions than simply holding a product. If this is true, then the shapes of containers could depend on which function is more important. Perhaps paying some cost in extra surface area means a higher profit for another reason. To know how important surface area is, we would like to know how much of a penalty in extra surface area it actually costs to make containers of different shapes.

Although the calculus provides a quick and easy way to find values for an optimum, it is not as easy to find out how a function is changing on either side of an optimum other than from the sign of the slope. Analytic geometry is useful for this because it shows more of the function.

Construct an *X,Y* coordinate system. Label the *Y*-axis as surface area (cm^2) and the *X*-axis as *h/r*. Include the origin ($X = 0$, $Y = 0$). Select the values of *h* and *r* for one of the containers you have measured and calculate the volume of that container in ml. You wish to know what surface area would be needed to make a container holding the same volume when *h/r* has different values (including the optimum value). Set the equation for volume equal to the volume you have calculated. Use a variety of numbers for *h/r* that span your data range and extend beyond it (e.g., include a value for *h/r* lower than your least and greater than the maximum from your data). Solve the *h/r*s for *h* (e.g., for $h/r = 3.0$, $h = 3.0\ r$), substitute the values for *h,* as numbers times *r,* into the equation for volume and solve for the *r*s. Once you know *r* you will also know *h* because you know *h/r*. Calculate surface areas using the values for *h* and *r*. Plot the surface areas as a function of *h/r* for that volume.

The shape of the function you have produced gives you information on the costs for not being optimal. To examine this specifically and quantitatively, calculate the percent increase in surface area that results for *h/r* values different from the optimum. The percent difference is calculated from the difference in surface area from the optimum divided by the optimum surface area for each *h/r* shape. Construct and label one function for *h/r* values *greater* than the optimum, and construct and label another function for *h/r* values *less* than the optimum, where you plot percent increase in surface area (*Y*-axis) versus the difference in *h/r* from the optimum (*X*-axis) for both functions. Start the *X*-axis at zero where the value for *Y* will be zero.

Do the two functions you have produced fall on the same line? What direction of variation from the optimum is most costly? Does your frequency distribution for h/r values seem to reflect the relative costs for variation in h/r on each side of the optimum? What feature of relative costs might explain why you do not find containers with more extreme values for h/r than you observed in your sample?

Assessing Cost Variation in Biology

The phenomenon we are studying here is quite common in biology. Animals often have to solve multiple problems to survive, and solving multiple problems can mean that a particular, isolated one may not be solved in the "best" way. Thus, the consequences for an animal should also depend on the costs for not being perfect if it must vary from an optimum to solve other problems. You may have experienced something similar in your academic career.

An example we have studied in lab is the "optimum" concentration for maximizing the rate of sugar gain by butterflies sucking sugar water through their proboscides. Use the same method you used above for studying the problem for optimal design of containers to quantitatively assess consequences for variation in sugar concentration for the butterflies. The points on the graph for this represent individual measurements, and you can assume that values along lines between the points are real. Include a graph for the butterflies in your report that is similar to the one you just made for the containers. Use this graph to predict what you think a butterfly should do when it is faced with problems that may require variation in what is "optimal" for nectar sugar concentration.

Notes for the Instructor: Exercise 1

Optimality Models in Biology

Understanding adaptations involves studying structures and functions to see how they influence organism performance. It is sometimes possible to predict a particular design that may maximize performance based on a criterion presumed to influence fitness. Empirical analysis (such as in Exercise 1), or mathematical methods (such as in Exercise 2), can be used to specify an independent variable thought to maximize performance. A combination of predictions based on models, and experiments to test predictions, provides an efficient way to understand adaptations. The book by McNeil Alexander (1982) gives a brief, excellent introduction to the approach with several examples. Examples include optimal structures for bone (hollow bones, like tubular scaffolding, provide maximum strength with least weight), flight, design of compound eyes, optimal mating tactics, and optimal foraging tactics.

There is controversy about the use of optimality ideas and models in science. For a wide variety of recent views, see the paper by Schoemaker (1991). Some argue the approach is tautological when it is used to try to prove organisms are adapted (Pierce and Ollason, 1987). I prefer to use the approach to test *how* organisms are adapted (Maynard Smith, 1978). Other criticisms concern the "realism" of the models (Rapport, 1991). Organisms are subject to historical, genetic, developmental, and environmental constraints often not reflected in the models (Dudley and Gans, 1991; Gould and Lewontin, 1979). The nature of models is simplicity. Biology is complicated. This is why I use quotation marks for "optimal." The exercises described here are meant to show that simple models can be used to help think about complicated problems, but they do not always work. This is progress because it forces revision of ideas and further experimental tests.

The approach has considerable pedagogical value. It provides a way for students to think about problems, and how to solve them, rather than memorizing facts. It provides a way for students to use simple analytical methods, such as graphs or algebra, so *they* can make predictions. As a consequence, they become interested in doing experiments. Finally, it provides some students a way to discover they have problems with very basic skills needed to solve problems.

Flow Through Tubes: Poiseuille's Equation

An important feature of models is they can be used to understand a variety of similar phenomena. Poiseuille's equation applies to laminar fluid flow through any rigid tube. It is most often used to understand flow through the vascular system, so the butterfly proboscis can be used as a model for vascular flow and vice versa.

The analogous problem for the vascular system is transport of oxygen via hemoglobin. As red blood cells increase in concentration, more oxygen is carried, but blood viscosity increases, so *net* oxygen delivery (what is carried minus the cost in oxygen to carry it) eventually decreases at high red cell concentrations (Hedrick et al., 1986).

Transport both through the butterfly proboscis and the vascular system can be generalized using Figure 5.1. Amount per ml for sugar or oxygen increases directly with concentration of sugar or hemoglobin, while viscosity increases non-linearly with concentration. The straight line represents the "benefit," while the curved line represents the "cost." Performance, or net transport, is maximized where benefit minus cost is greatest. This is shown with the double arrow in Figure 5.1. The predicted maximum occurs at an intermediate concentration.

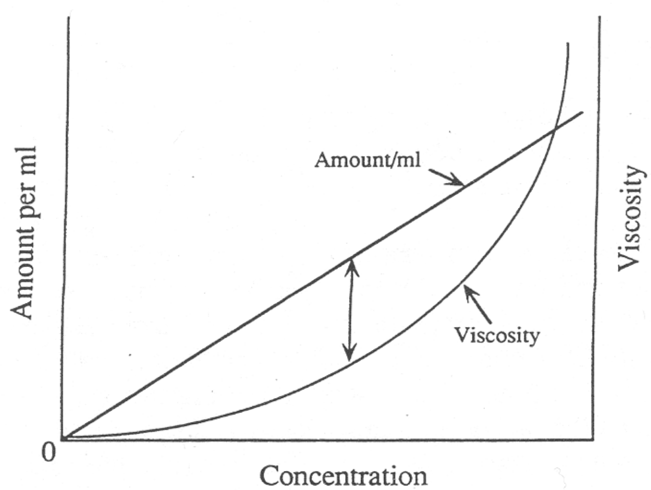


Figure 5.1. Amount per ml and viscosity as functions of concentration to illustrate how the difference between the two is maximum at an intermediate concentration (shown with the double arrow). This figure can be used to show what is important for net transport with fluids through any tube.

Butterfly Ingestion

Mixing Solutions and Calculating Solution Specific Gravities: Example for 50% Sucrose

For a 50% solution we wish to have 50 g of sucrose in a total solution volume of 100 ml. The specific gravity of pure sucrose is 1.588 g/ml. Dividing this into 50 g gives 31.49 ml, so the sucrose will occupy 31.49 ml in the 100 ml solution. The remaining volume must be water, so 100 - 31.49 = 68.51 ml, is the volume of water to add to 50 g of sucrose for a final solution volume of 100 ml.

The specific gravity of the 50% solution is its total mass divided by 100 ml. We know the mass of sucrose is 50 g. One ml of water has a mass of 1.0 g, so the total mass of the 50% solution is 50 g + 68.51 g = 118.51 g. Dividing by 100 ml gives a specific gravity of 1.1851 g/ml for 50% sucrose. Table 5.1 gives the specific gravities for each solution students will feed to butterflies. You can use these values to check student calculations. Errors most often involve not keeping track of units in the calculations. If you find errors, the first place to check is the units on numbers.

Table 5.1. Specific gravities of sucrose solutions.

Percent sucrose	g/ml of solution
8.75	1.0324
17.5	1.0645
35.0	1.1296
50.0	1.1851
80.0	1.2962

Feeding Butterflies

Instruct students to pick up a butterfly that is not flying. Once it is grasped with index and middle fingers, it can be repositioned and held between thumb and index finger. Be sure all four wings are held. Once students start working with the butterflies, a "bond" seems to develop, and students are usually very careful with them. Wing wear is usually the only limit for butterfly longevity in the lab. Even with student handling we have been able to use the same butterfly for up to three separate lab sessions.

Calculating Volume Ingestion Rates: An Example

Solution specific gravities (Table 5.1) are used to calculate the volume ingested from the change in mass of a butterfly. It is least confusing to first use the mass change to convert it to a volume, and then divide the volume by time to get the rate. It also is least confusing to keep the mass change units as grams (rather than using milligrams) because specific gravity values the students use are in g/ml.

For example, a butterfly changed mass by 0.0297 g when it fed for 120 seconds using 8.75%

$$\frac{0.0297\ g}{1.0324\ g/ml} = 0.028768\ ml$$

sucrose. Dividing 0.0297 g by the specific gravity of 8.75% sucrose gives

Note that it is important to use the specific gravity of *the solution fed to the butterfly*. Students often use 1.588 g/ml because they see the units work, but each solution has a different specific gravity, and none are pure sucrose.

A volume in ml can easily be converted to µl and then to nanoliters by moving the decimal three places to the right for each conversion. For the example the volume ingested is 28.768 µl or 28,768 nanoliters. Because nanoliters are in magnitudes of tens of thousands, it is important for students to carry out the calculation of volumes in ml to six decimal places.

Now the volume in nanoliters should be divided by the ingestion time in seconds. For this case the volume rate of ingestion is 28,768 nanoliters/120 seconds = 239.7 nanoliters/second.

Calculating Sugar Rates of Ingestion

As explained in the Student Outline, each solution contains the amount of sucrose as µg/nanoliter when percents are expressed as fractional amounts. Thus, 8.75% sucrose contains 0.0875 µg/nanoliter, 80% sucrose contains 0.80 µg/nanoliter, etc.

Multiplying nanoliters/second times µg/nanoliter gives µg/second; so for our example, 239.7 nanoliters/second × 0.0875 µg/nanoliter = 21.0 µg/second – the rate of sugar ingestion with the 8.75% solution.

Students become very adept at these calculations once they have done them correctly. We always ask to check their first set of calculations to prevent time consuming errors. The easiest way to check calculations is to pay attention to units and to be sure the students use the appropriate value for solution specific gravity.

Making Graphs

Figure 5.2 shows typical results for average volume rates of ingestion, and Figure 5.3 shows typical results for average sugar rates of ingestion. There will be some variation in the averages depending on how long butterflies are allowed to feed. Very short (less than 30 seconds) or very long (more than 4 minutes at low concentrations) feedings may give lower rates. Sometimes the first feeding shows a lower volume and sugar rate than subsequent feedings. The errors associated with the measurements will vary depending on the sample size used to calculate the averages. Visual inspection of averages and confidence intervals shows 35% and 50% sucrose are unlikely to be statistically different for rate of sugar ingestion. Even if you do not calculate errors for measurements, the averages for these concentrations are likely to be similar enough that students will appreciate there is little difference between them. Which concentration is used as "optimal" for the choice experiments is an interesting question to stimulate discussion.

Is there an "optimal" concentration for a maximum rate of sugar ingestion? Why? (Consider the slopes for volume rate and for sugar amount as a function of concentration.) Mathematically, the maximum rate will be somewhere between 35% and 50% sucrose. How to decide what it is provides interesting discussions, for example, should we do more experiments, or could we find out by drawing a curve through the points? Which of these would be easiest? Students should be encouraged to think about how the relationships in Figure 5.1 are related to what they have produced
in both of these figures.

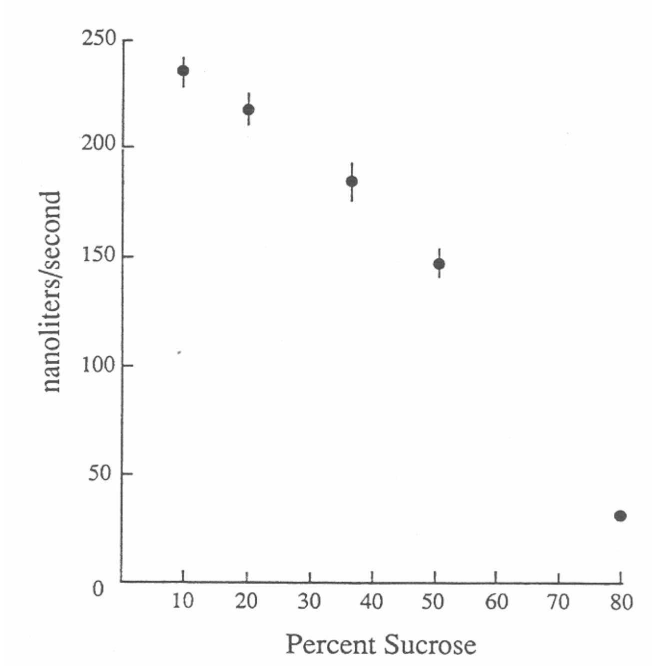


Figure 5.2. Typical results for average rate of volume ingestion as a function of sucrose concentration. This demonstrates the importance of viscosity for flow.

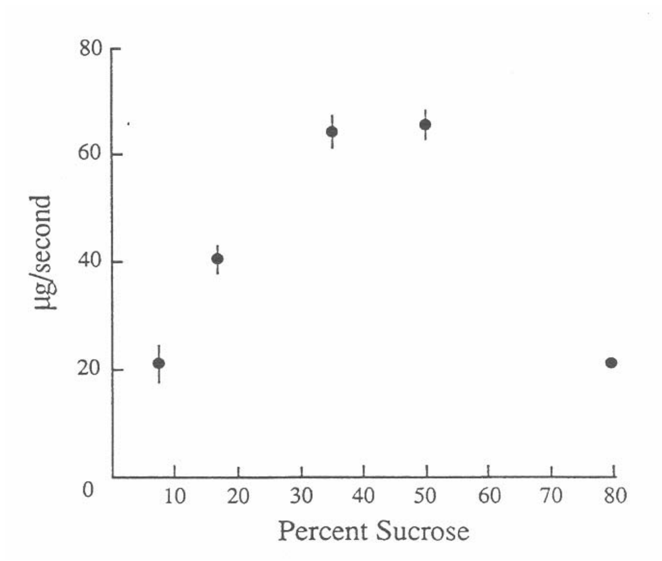


Figure 5.3. Typical results for average rate of sugar ingestion as a function of sucrose concentration.

Pipetting by Humans

You may or may not get similar results to the results for butterflies depending on the type of pipet you use. Small bore pipets are most likely to give similar results. But I do not think it is important to have to duplicate the results as found for butterflies. You may wish to use pipets with a large bore just so students will *not* see what they expect. This will force them to think about what is different between butterflies and pipets. We constantly try to get students to expect the unexpected and to pay attention to measurements that are unexpected as something *interesting*. This simple exercise provides such an opportunity. Perhaps you can have some students use one type of pipet, and others another, so you can compare results.

With large-bore pipets average volume rates of ingestion typically do not decrease appreciably as concentration increases. Consequently, sugar rates of ingestion will increase directly with concentration. For this situation an "optimal" concentration is the highest concentration.

How do your results compare with those for the butterflies? Is the "optimal" concentration for either sharply defined, that is, are the functions narrow and peaked, or are they broad and flat (are adjacent average values statistically different based on 95% confidence intervals)? How might the shape of a function influence the way you interpret what butterflies or humans should do? The answers obviously depend on the results. These questions are designed to have students begin to think about how the shape of an optimal function, as produced for butterflies, might influence organism performance if an organism must vary in its performance. This is the major feature for Exercise 2. Introducing the main questions at this point provides an important connection between the two exercises.

Choices by Butterflies

To stimulate students to think about choices between "fast food" and "haute cuisine," we ask them to visualize going to a fast food restaurant and ordering one of two items: (1) a very thick milk shake, or (2) a soda. They are told they must ingest their choice with a straw. They are asked which one they would order if they were *very* hungry. They also are asked which one they would order if they were *really* in a hurry.

The proboscis is quite flexible, so the choice is easy to see even when the dishes are almost touching. Some butterflies extend the proboscis directly down, and then probe toward one side. It is important to wait between trials until the proboscis is retracted so there will be time to position legs in both dishes before the butterfly tries to feed again. The reason for placing 80% sucrose in the least preferred position is to make it more likely to identify a preference in a fixed number of trials.

Analysis

The binomial expansion looks formidable, but it only involves multiplying and dividing. Calculators with exponent keys are important. It helps if students try to calculate the examples given in the Student Outline. This is a quick way to check that they know how to use their calculators.

Errors are most likely when steps are missed. To help check for problems we always ask students to take the time to *write out each step* in a series of calculations. This makes it easier to find problems, such as not knowing *X!* means "*X* factorial" and not "wow an *X*!"

How do you interpret the results (for your lab report Discussion section)? What is an "optimal" concentration for butterflies based on your results? Why? (Think about time and energy.) Some biologists think that plants should have evolved to produce nectar to attract butterflies so the plants can be ensured of being visited and pollinated. What concentration would you predict for this based on your results? The average sugar concentration for nectars from plants pollinated by butterflies is about 35% sucrose, and it ranges from 10% to 65% sucrose. How do you interpret concentrations produced by plants based on your measurements and experiments? Students are encouraged to think of how what a butterfly selects might be "optimal" in different situations. Perhaps energy is more important when they are hungry. Perhaps time is more important when they are not. Some experiments suggest the most concentrated sugar is preferred (Hainsworth, 1989), but this does not have to always be the case for a single butterfly during the exercise. The questions about nectar concentrations are designed to have students think about where butterfly food comes from, how alternative foods can influence choices, as well as what can be "optimal" in different situations.

Quiz Material

We allow students to take quizzes "open book" by using their notes. After the first week this dramatically improves the quality of notes. For this exercise students are asked to calculate the specific gravity of a solution of 70% sucrose. They also are asked to calculate the volume and sugar rates of ingestion for a butterfly that consumes 70% sucrose so it has changed weight by 0.0055 g after feeding for 90 seconds.

Notes for the Instructor: Exercise 2

Calculating a Prediction

Predictions Using Calculus

Figure 5.4 summarizes the geometry and calculus. It can be used for making a transparency.

$$h/r = \frac{V}{\pi r^3}$$

$$r^3 = \frac{V}{\pi (h/r)}, \text{and}$$

$$r = \left(\frac{V}{\pi (h/r)} \right)^{0.33}$$

A useful short-cut for calculating *r* with different values for *h/r* is to solve for *r*, so
Volume (*V*) is a constant, so simply substituting different values for (*h/r*) and taking cube roots is a quick way to find *r*s.

Predictions Without Calculus and Graphs of Surface Area versus *h/r*

There is a simple way to arrive at the prediction that involves a few steps of algebra and construction of a graph. The graph is used regardless of the method used to obtain the prediction, but it is used at different times depending on the prediction method.

For a cylinder,

$$V = (\pi r^2)(h), so$$

$$h = \frac{V}{\pi r^2}, and$$

$$h/r = \frac{V}{\pi r^3}, so$$

$$r^3 = \frac{V}{\pi (h/r)}, and$$

$$r = \left(\frac{V}{\pi (h/r)}\right)^{0.33}$$

You can explain an interest in looking at *h/r* by suggesting it may provide an index to the shapes of containers regardless of their volumes.

You can now have students select one cylinder, measure *r* and *h*, and then calculate *V*. Volume is used as a constant in the last equation. Next they calculate values for *r* using the last equation for the cases *h/r* = 0.1, 0.5, 1.0, 2.0, 3.0, 4.0, and 5.0. Values for *h* are found from the *r*s (e.g., for *h/r* = 4.0, *h* = [4.0][*r*]). They now can calculate surface areas ($2\pi rh + 2\pi r^2$) for each *h/r* shape to construct a graph of surface area on the *Y*-axis and *h/r* on the *X*-axis. The minimum is at *h/r* = 2.0 by inspection.

As an example, consider a soda or beer can with *h* = 11.3 cm and *r* = 3.15 cm. $V = 352.2\ cm^3$,

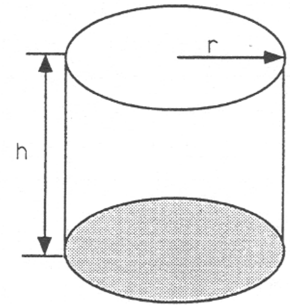
$$r = \left(\frac{352.2}{\pi (4)}\right)^{0.33} = 3.04\ cm$$

and for the case *h/r* = 4.0,

Thus, *h* = 12.16 cm, and surface area = 290.3 cm^2. Table 5.2 shows surface areas for different *h/r* values for this container, and Figure 5.5 shows surface area as a function of *h/r*.

If the non-calculus method is used it is important to produce the graph, such as Figure 5.5, *before* students measure the containers to construct the frequency distribution of *h/r*. This is important so they will have a reason to look at *h/r* values for the containers. With calculus the prediction is evident without the graph, so they should construct the *h/r* frequency distribution for containers first, and then select one container to produce the surface area versus *h/r* graph to ask questions about costs for variation.

It is very interesting that many students who have taken calculus have seldom used it to make a prediction they can test like this. They seem really impressed when they see from the graph that it actually works! Also, for instructors using either approach, checking to see that the minimum surface area occurs at *h/r* = 2.0 is an efficient way to check for errors in calculations. We ask students to start by calculating surface areas for *h/r* = 1.0, 2.0, and 3.0 first to check for this.



$$\text{Surface Area} = 2\pi r h + 2\pi r^2$$

$$\text{Volume} = \pi r^2 h$$

$$h = \frac{V}{\pi r^2} \quad \text{and} \quad \frac{h}{r} = \frac{V}{\pi r^3}$$

$$A = \frac{2V}{r} + 2\pi r^2$$

$$\frac{dA}{dr} = \frac{-2V}{r^2} + 4\pi r$$

$$\frac{d^2A}{dr^2} = \frac{4V}{r^3} + 4\pi$$

$$\text{For } \frac{dA}{dr} = 0$$

$$r^3 = \frac{V}{2\pi}$$

$$\frac{h}{r} = 2$$

Figure 5.4. Summary of the geometry and calculus for the problem of optimal design of a cylindrical container.

Table 5.2. Surface areas for different shapes for a soda or beer can.

Surface area (cm^2)	*h/r*
746.1	0.1
347.3	0.5
291.9	1.0
276.5	2.0
280.4	3.0
290.3	4.0
299.8	5.0

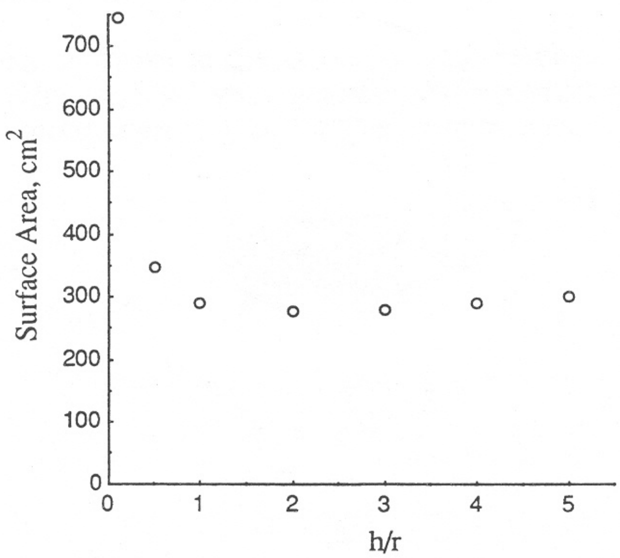


Figure 5.5. Surface area as a function of *h/r* for a soda or beer can showing how the minimum, at *h/r* = 2.0, can be found by inspection.

Testing the Prediction

Figure 5.6 shows a frequency distribution for 83 unique cylindrical containers.

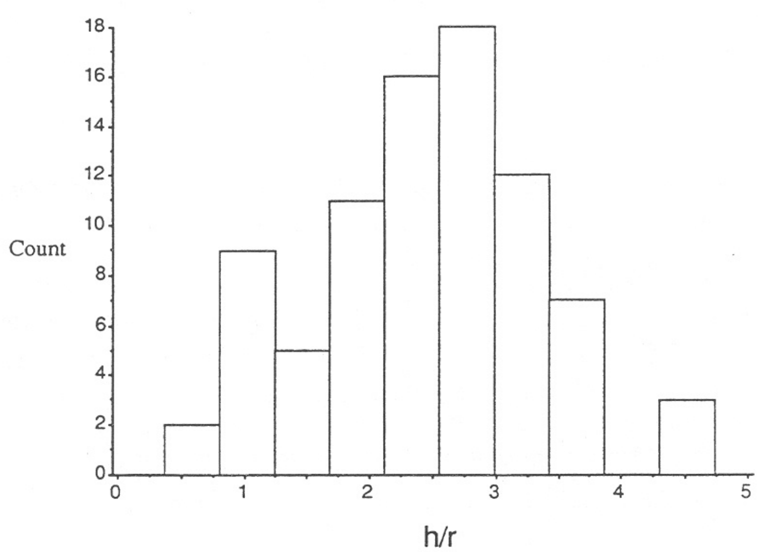


Figure 5.6. Frequency distribution of *h/r* values for 83 uniquely different cylindrical containers obtained from trash containers in Syracuse, New York.

How are your data for unique containers distributed with respect to your prediction? Is the distribution symmetrical, that is, are there about the same number of h/r values above and below the predicted optimum? How about above and below the average for h/r? Are the average, median and mode for h/r at the same category interval on the distribution? Whether you see symmetry depends on your containers. If you find very tall, thin containers, it will skew the distribution toward high values for *h/r*. Both the average and the mode for the data in Figure 5.6 are above *h/r* = 2.0, so more measurements are found above the predicted value than below.

A variety of hypotheses are possible for why containers may not be "optimal" for minimum surface area. Shelf space in stores may be at a premium, so more containers could be displayed using a taller, narrower container. Perhaps consumers perceive tall, narrow containers to contain a larger volume.

Assessing Variation in Cost

If you follow the calculus method you should have the students construct the graph (Figure 5.5) at this point. Figure 5.7 shows the percent change in surface area as a function of difference in *h/r* from the optimum for the data shown in Figure 5.5.

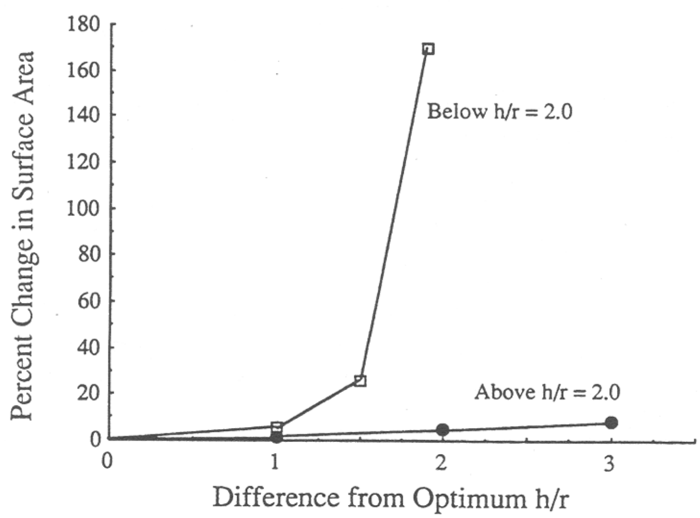


Figure 5.7. Percent change in surface area as a function of difference from the optimum for a soda or beer can.

Do the two functions you have produced fall on the same line? What direction of variation from the optimum is most costly? Does your frequency distribution for h/r values seem to reflect the relative costs for variation in h/r on each side of the optimum? What feature of relative costs might explain why you do not find containers with more extreme values for h/r than you observed in your sample? They do not fall on the same line, and *h/r* values less than 2.0 are more costly. The relatively low cost for *h/r* > 2.0 can be used to discuss why most containers may be found in this part of the frequency distribution. Why businesses make containers with *h/r* < 2.0, such as cat food and tuna fish cans, is a puzzle, but you can see that even more extreme values for *h/r* < 2.0 than these would be very costly.

Assessing Cost Variation in Biology

Figure 5.3 is relatively symmetrical, so costs for variation from the maximum will be about the same in each direction from the maximum. Also, the function is relatively “flat” near the maximum, so butterflies could experience a bit of variation in either direction and still achieve sugar ingestion rates close to the maximum. To focus on this feature, you can instruct students to figure out what the total variation in percent sucrose is around the maximum for a 5% change in the maximum rate of sugar ingestion.

Quiz Material

The “open book” quiz for this exercise asks the students to calculate the volume of a container of given height and radius. They also are asked to calculate what the surface area of that container would be if $h/r = 4.0$.

Materials: Exercise 1

All materials are per experimental group except where noted.

Adult Painted Lady butterflies (3–4)
“Butterfly Habitat” plastic containers (Carolina #L-919H) (2)
Plastic beakers, 50-ml (Fisher 2-544-38, 500/pack, $75.00 US/pack) (15–20)
Masking tape
Sucrose, 85 g
Triple-beam balance (0.1 g resolution) (1)
Spatula (1)
Powder funnel (1)
Polypropylene bottles (125 ml) with screw on lids (Cole Parmer #YB-06048-10, $13.68 US/pack of 12) (5; 1 contains pre-mixed 80% sucrose)
Graduated cylinder, 100 ml (1)
Stopwatch (0.1-second resolution) (1)
Analytic balance (0.0001 g resolution) (1 per 2 groups)
volumetric pipet, 3 ml or 5 ml (1)
Scissors (1)
Macintosh computer (1) with Statview Student software (Abacus Concepts, Inc., P.O. Box 2030, Shingle Springs, CA 95682; 1-800-241-8443; $100 US/copy list. Call for quote and discount). Other computers with descriptive statistical software may be substituted. Without computers you will need graph paper and a calculator (to calculate averages).

1. Butterflies can be ordered from Carolina Biological either as chrysalides (#L-912A, $3.83 US each) or as larvae with food to raise them (#L-916, “Painted Lady BioKit Refill,” 60–80 larvae, $52.25 US). Larval food must be spooned into small cups (supplied) so they are 0.33 to 0.5 full. You need to add 1" filter paper discs to the inside of the cup lids. These are *not* supplied with the order. Place two larvae/cup. Chrysalides form in 10–12 days, when they will hang from the filter paper, and they can be moved to “Butterfly Habitat” containers (12 each). Place absorbent towels on the bottom to blot fluid produced when the adults emerge. It takes another 10 days for adults to emerge. A very nice feature is adults can be kept in a refrigerator (5°C) unfed for

up to 3 weeks. You can minimize timing problems with the lab by ordering larvae well in advance, and keep adults in the refrigerator until shortly before they are needed.

2. Heat the 80% sucrose to get it to dissolve quickly.
3. The pipets mimic butterflies best when they have a narrow bore. Fisher supplies a 100-ml viscometer pipet (#13-625, $33.45 US each), but this will require mixing larger volumes of sucrose. Large bore pipets, such as the plastic disposable types, do not mimic butterflies well because of the importance of tube radius for flow. This feature can be used as part of the design for this exercise (see Notes for the Instructor, Exercise 1).
4. If you do not use a computer, students should have calculators to calculate averages, and graph paper to construct graphs by hand.

Materials: Exercise 2

Cylindrical containers (50–100 per 2 groups)
Calculators with an exponent key
Tape measures (1 mm resolution) (1 or 2)
Graph paper
Macintosh computers with Statview Student software (see Exercise 1), or other computers for producing frequency distributions, or graph paper to make frequency distribution graphs by hand.

1. Cylindrical containers can be made of any material. The only restriction is that shape not be a function of contents. Thus, you should not use tall containers designed to hold a stack of potato chips, or broad, flat containers designed to be used as a serving dish. For glass containers, students should be instructed to ignore the top screw-on area where a lid was attached. Containers can be obtained from supermarkets or by raiding your neighbor's trash. Leave the labels on as this seems to stimulate interest by the students in what they are measuring.
2. The exponent key on the calculator is important to calculate cube roots (0.3333 power) to solve for r with different values of h/r (see Notes for the Instructor, Exercise 2).
3. If computers are not used, students should search their data for duplicate h and r values as they collect the data. Graph paper will be needed for frequency distributions and surface area graphs.

Acknowledgements

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