Chapter 4

Principles of Allometry

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Introduction

In this computer-assisted exercise students explore the fundamental concept of allometry (the study of size and its consequences), examine the relationship between size and shape, and learn how to quantify changes in proportions. Specifically, they investigate how mammals of various sizes change proportions to compensate for changes of surface area and volume. Interactive computer programs aid each student in calculating standard dimensions from an illustration of an animal, process class data, identify lines of best-fit (using linear regression), and statistically test whether relationships between selected morphological variables exhibit isometric or allometric change.

This 3-hour laboratory exercise has been used in the introductory biology course at the University of Toronto (BIO110Y – The Nature of Living Organisms) annually since 1984/85. The interactive computer programs that accompany this exercise were introduced in 1986/87 and 1987/88 and are available as user-supported "shareware" (see Appendix D). At the University of Toronto this exercise is performed each year by 400 students during a 1-week period (20 students per laboratory room, 80 students per laboratory time).

The activities in this laboratory do not require that students have taken a prior course in biology, however there is a heavy emphasis on the manipulation of quantitative data. We assume that students have been exposed to graphing techniques, logarithms, determination of rates of change from graphs, and Student's *t* test. At the University of Toronto this information is contained within a self-study manual (Goldman, 1987) which introduces the scientific method and "how to" collect, organize, analyze, interpret, and present the numerical data that students obtain in the laboratory.

This exercise defines allometry, allometric change, and isometric change, and emphasizes the importance of the ratio of surface area to volume (i.e., simply by growing larger the surface area of an object will continually decrease relative to its volume if its shape remains unchanged). Students are required to complete (before the laboratory) a problem which relates to the ratio of surface area to volume. An introduction to allometric equations, the allometric coefficient, log-transformations, linear regression, and dimensional exponents enables students to determine if a relationship exhibits isometric or allometric change. In Part 1 students calculate surface area and volume from simple geometric shapes. In Part 2 they investigate the relationship between the "size" of selected North American mammals and (1) minimum leg cross-sectional area and (2) the ratio of surface area to volume. Students present the results of their investigations from Part 2 in a formal laboratory report which is due the following week.

For the instructor there are two important books that provide an introduction to the importance of animal size and the basic principles of allometry: *Scaling: Why is animal size so important?* by Schmidt-Nielsen (1984) and *On size and life* by McMahon and Bonner (1983). Additional references include Calder (1984), Gould (1966, 1977), Peters (1983), Reiss (1989), Schmidt-Nielsen (1975), Smith (1980), and Sweet (1980).

Notes for the Instructor

Materials (per 20 students)

- 1. IBM-compatible XT/AT computers (minimum of two for 20 students) with at least a monochrome (Hercules-compatible) graphics card and a 5 1/4" (360 KB) or 3 1/2" (720 KB) floppy disk drive; a hard disk drive is desirable, but *not* mandatory. The programs are only available for IBM-compatible computers.
- 2. Dot-matrix printers (one per computer) and computer paper (9 1/2" x 11" perforated, continuous sheets).
- 3. Set of 26 different mammal illustrations.

Photocopies of the color engravings in *The Art of Audubon: The Complete Birds and Mammals* (John James Audubon, Times Books, 1979; ISBN 0-8129-0841-4) are excellent since the illustrations are large and the entire animal is viewed unobstructed and from the side. For permission to reproduce these engravings contact: Random House, Inc., 201 East 50th Street, New York, NY 10022, Attention: Permissions Department (27th Floor).

Twenty-six selected mammals (including the bison—used to demonstrate CALCULATOR program) from *The Art of Audubon* are (page number, scale factor), in increasing size:

```
star-nosed mole (535, 1:2.5)
                                                     porcupine (550, 1:3.8)
lemming (548, 1:2.2 [rear], 1:2.4 [fore])
                                                     raccoon (588, 1:4.3)
field mouse (581, 1:1.8)
                                                     otter (566, 1:4.8)
meadow vole (516, 1:3.0)
                                                     black wolf (521, 1:11.0)
wood rat (585, 1:2.2)
                                                     red wolf (525, 1:8.9)
long-tailed weasel (599, 1:3.0)
                                                     cougar (543, 1:8.8)
Albert's squirrel (613, 1:2.8 [left])
                                                     pronghorn (505, 1:17.2)
shorttail weasel (601, 1:3.4)
                                                     mountain goat (527, 1:18.9)
ground squirrel (637; 1:2.6)
                                                     blacktail deer (530, 1:14.3 [fore])
yellow-bellied marmot (510, 1:3.5)
                                                     moose (534, 1:27.8)
muskrat (546, 1:2.7 [animal at right])
                                                     elk (540, 1:19.9)
jackrabbit (554, 1:2.4)
                                                     polar bear (652, 1:12.2)
peccary (539, 1:6.1)
                                                     bison (519, 1:20.7)
```

- 4. 20 vernier calipers and/or 20 metric rulers (clear, minimum of 20 cm in length).
- 5. 60 sheets of white bond paper: $8 \frac{1}{2}$ " × 11", light weight suitable for tracing.

- 6. Three computer programs: (a) CALCULATOR aids each student in calculating standard dimensions from their mammal illustration; (b) CLASSDATA processes the class data to be used in the student's assignment; and (c) REGRESSION identifies lines of best-fit using linear regression and statistically tests whether the relationships between selected morphological variables exhibits isometric or allometric change. These programs are available as user-supported "shareware" (see Appendix D).
- 7. 10 sets of three-dimensional acrylic geometric shapes (one set for two students).

The seven shapes (dimensions in Appendix F) are as follows: cube, short rectangular solid, long rectangular solid, short cylinder, long cylinder, pipe, and sphere. Acrylic rods of each specific shape can be purchased from a local plastics supply company and cut to size either by the supplier or in-house. [In Toronto: Warehoused Plastic Sales Inc., 13 Blackburn St., Toronto, Ontario M5M 2B3, (416) 465-3591] NOTE: If acrylic shapes cannot be obtained, students can measure two-dimensional shapes drawn on paper.

- 8. Copy of table to record class data for entry into CLASSDATA program; including student's surname, name of animal, surface area (dm²), volume (dm³), SIZE (dm), and minimum-leg cross-sectional area (cm²) for each animal.
- 9. Students are required to bring their own calculator to the laboratory.

Procedures

- 1. In Part 1 students measure seven acrylic geometric shapes (and entering these data in Table 4.2). Measuring these shapes will give students much needed practice *before* they measure the shapes from their mammal illustration. Values are given in Appendix F.
- 2. Each student will calculate dimensions from one mammal illustration. To simplify taking measurements students may wish to (a) trace shapes onto a second sheet of paper (easier to read measurements) and (b) use calipers to make measurements directly from the page (easier to read than from a ruler). Students should be encouraged to read Appendix C very carefully. They must first convert from "size of drawing" to "actual size of animal" (multiplying by scale factor given on illustration) before calculating dimensions. Decimeters are used in order that size is expressed in values that are meaningful; for example, the surface area of a bison is approximately 872 dm² or 87,200 cm², the latter appears excessively large.
- 3. CALCULATOR (by David Brown, Corey Goldman, and Richard Snell) assists in the calculation of surface areas (SAs) and volumes (VOLs) of simple and complex geometric shapes (sphere, cylinder, cone, spheroid, frustum); thus eliminating time-consuming calculations and greatly reducing errors.

Specifically students are to calculate the SA, VOL, SIZE, and minimum-leg cross-sectional area (MLXA) of a selected North American mammal based on the dimensions taken from their Audubon illustration (scale provided on illustration). Once measurements are recorded from the illustration and manipulated they are entered into the program as requested. CALCULATOR generates a "picture" to "double check" the entry of data and prints for each student a

"computer-copy" of their mammal illustration and a printed summary of the results. The instructor can demonstrate how the program operates by entering data for the bison (see Appendix G); sample output is provided in Appendix H.

4. CLASSDATA (by David Brown and Corey Goldman) assists in the collection and distribution of class data.

At the end of the laboratory the instructor enters the following for each student: student's surname, student number, name of animal, and four variables (SA, VOL, SIZE, and MLXA). The instructor can add, delete, change, display, sort, print, or plot the data at any time. CLASSDATA prints all data as entered and calculates four additional variables (SA:VOL and three log values) for each entry; these data are used in the student's assignment. Photocopies of the class data table are distributed to students the following day.

5. REGRESSION (by Jeff Thomason) utilizes linear regression in order that students can find a line of best-fit to data plotted as y versus x, and tests whether the relationship between morphometric variables exhibits isometric or allometric change [by (a) predicting the isometric slope (and then performing a t test to determine if the actual slope of the regression line is significantly different to the predicted isometric slope), and (b) using the 95% confidence limits of the actual slope].

Students enter paired data (x, y); entry of the predicted isometric slope is optional. Printed results include: data necessary to plot regression line and upper and lower 95% confidence limits, slope of the regression line and 95% confidence limits, summary of the t test of calculated versus predicted slopes, and raw and log-transformed data. REGRESSION prints a final plot of the data on the screen to allow students to check the entry of data and illustrate what their plot should look like; this plot cannot be printed on the dot-matrix printer (the intent is to give students practice at graphing).

NOTE: Due to insufficient time and an insufficient number of computers it is *not* recommended that students use REGRESSION during the 3-hour laboratory period. At the University of Toronto a computer room is open for several hours each day for student use. Although the results of the regression program will be the same for all students within a class, every student should be encouraged to use REGRESSION, either independently or in pairs. Each student uses the program twice: to investigate the relationship between (a) MLXA and SIZE, and (b) SA:VOL and SIZE.

7. Appendices A to C are to be included in the outline for the students. Appendices D to H are for the instructor.

Student Outline

Introduction

The diversity of living organisms is astounding. However, despite many peculiarities, a striking "lawfulness" in the basic design of organisms is evident—largely the correlation of size and shape. Animals are physical objects and are shaped to their advantage by natural selection. Consequently, they must assume forms best adapted to their size.

Blue whales, the largest animals, are aquatic and are able to attain their great size only because they are supported by the water in which they live. If a bird is to fly, its weight, which is directly related to its size, tends to remain below a certain limit. Therefore, it is not surprising that all very large birds, such as ostriches, emus, and dodos, lost the art of flying. Why are there "flying" squirrels but no animals the size of elephants that climb trees and glide about on webs of skin stretched between their appendages? Why are the smallest mammal (the dwarf shrew) and the smallest bird (the Cuban Bee Hummingbird) both about the same length (4 to 5 cm) and weight (approximately 3 g)?

In this laboratory you will examine the relationship between the size and shape of organisms and learn how to measure changes in proportions. This will be done by measuring change in shape without changing volume (Part 1), and examining changes in size and shape of mammals (Part 2). Both the collection and analysis of data for Part 2 will be aided by computer programs.

Allometry

Changes in size and shape were understood in a general way, but they were difficult to measure in a useful fashion, until Julian S. Huxley, the well-known British zoologist, and (independently) the French zoologist Georges Teissier developed the method of "relative growth" or allometry.

Allometry describes the relationships between dimensions of organisms and changes in the relative proportions of these dimensions with changes in absolute size. The term refers to comparisons between individuals of the same species (intraspecific) and among different species (interspecific). For example, not only are the proportions of a chick quite different from those of a hen, but the proportions of a hen are quite different from those of an eagle.

Length, Surface Area, and Volume

Imagine two organisms of which the smaller is an exact scale model of the larger. If the larger is n times as long as the smaller, any organ of the larger is n times as long, n times as broad, and n times as thick as the corresponding organ of the smaller organism. The organs must therefore have n^2 (n × n) times the surface area (denoted SA) and n^3 (n × n × n) times the volume (denoted VOL) of the corresponding organ in the smaller organism. (This occurs because SA increases as the square of length [denoted L; L × L] and volume increases as the cube of length [L × L × L].) If they are constructed of the same materials, the weight of the larger organism is n^3 times the weight of the smaller organism, since weight is proportional to volume. Thus, in these organisms (∞ = is proportional to):

$$SA \propto L^2 \text{ (or, } L \propto SA^{0.50})$$

$$VOL \propto L^3 \text{ (or, } L \propto VOL^{0.33})$$

$$SA \propto VOL^{0.67} \text{ (or, } VOL \propto SA^{1.5})$$

As will be demonstrated, in this elementary example lies a principle of profound biological significance.

Ratio of Surface Area to Volume

Consider the change in the ratio of surface area to volume (denoted SA:VOL) in a series of cubes of different sizes (Table 4.1). SA increases in proportion to the square of the length, and VOL is proportional to the cube of length. Observe what happens to SA:VOL. Simply by growing larger the surface area of any object will continually decrease relative to its volume when its shape remains unchanged. Why is this important to animals?

I anoth of side	SA	VOL	SA:VOL
Length of side		$VOL_{\frac{3}{3}}$	*
ст	cm ²	cm³	cm ⁻¹
1	6	1	6.00
2	24	8	3.00
3	54	27	2.00
4	96	64	1.50
5	150	125	1.20
6	216	216	1.00
7	294	343	0.86
8	384	512	0.75
9	486	729	0.67
10	600	1000	0.60

Table 4.1. Relation of surface area (SA) and volume (VOL) in a series of cubes.

Many bodily functions depend upon SA:VOL. For example, both heat and water exchange occur across surfaces of animals. In the evolution of large and complex organisms, the specialized development of internal organs has been particularly important as a compensatory mechanism for the relative decrease in surface area. For example, the highly convoluted surfaces of the alveoli (air-filled sacs) of the lung promotes efficient gas exchange; similarly, the villi (finger-like projections) of the small intestine increase the relative surface area available for the absorption of nutrients.

Some simpler organisms have never evolved internal organs and in becoming larger, important restrictions have been placed on their shape. For example, a tapeworm may be 7 m in length, but its thickness cannot exceed a fraction of a centimeter because food and oxygen must penetrate from external surfaces to all parts of the body.

Other organisms are constrained to remain small. Why are there no very large insects (with the exception of those in B movies)? A factor which contributes to the limitation of size is the method insects use to respire. In insects, air is carried directly to the tissues by diffusion through a series of tubes—the trachea and tracheoles. (Insect blood plays no role in oxygen transport.) The volume of oxygen supplied by the tracheal tubes is proportional to the cross-sectional area of these tubes, but the cross-sectional area does not increase in proportion to the insect's body weight. Because diffusion distances are greater in larger insects, oxygen supply is consequently proportionally reduced and thus body size is limited.

The principle of adjusting bodily proportions with increasing size may well be the most important determinant of the shape of organisms. J. B. S. Haldane (1927:21) once wrote that "comparative anatomy is largely the story of the struggle to increase surface in proportion to volume." Stephen J. Gould (1977:178) ended an essay on size and shape with the following:

"I once overheard a children's conversation in a New York playground. Two young girls were discussing the size of dogs. One asked: `Can a dog be as large as an elephant?' Her friend responded: `No if it were as big as an elephant, it would look like an elephant.' How truly she spoke."

Allometric Versus Isometric Change

Allometric change occurs when the proportions of an organism *adjust* to the different rates at which surface area, volume, and other physical parameters change with differing sizes. It is sometimes referred to as differential scaling.

Isometric change occurs when each dimension of an organism is scaled up or down regardless of the disproportionate change in such parameters as surface area and volume. If x doubles in length, then so does y. The proportions remain constant and do not change with a change in size. McMahon and Bonner (1983) suggest that an easy way to picture this in one's mind is to think of a photographic enlargement. If it is a photograph of a horse, then the horse's proportions remain the same whether one looks at a small contact print or a big enlargement. A simple example of isometric change is provided by the series of cubes of different sizes discussed above. Isometric change is sometimes referred to as geometric similarity.

(The term *allometric* means literally "by a different measure", from the Greek *allois*, different. By contrast, *isometric* means "by the same measure.")

Problem

Before proceeding further answer the following problem which relates to SA:VOL. This problem will be discussed by your instructor at the *beginning* of the laboratory.

A multicellular, spherical, aquatic organism has a central cavity containing water. It does not exchange oxygen with this central fluid. The radius of the entire organism is 2 cm, and the radius of the central cavity is 1.5 cm. This organism can obtain enough oxygen from the water surrounding it if the dissolved oxygen in the water equals 4 ml per liter. Could the same organism grow to have a radius of 4 cm if the oxygen concentration of the water were increased to 6 ml per liter? Consider what would happen both in a situation of isometric and allometric growth (that is, in one instance the layer of cells becomes 1 cm thick, while in the other the

layer of cells remains 0.5 cm thick.) Give reasons for your answer and show all your calculations. (Consider only the external surface area and assume that the cytoplasm is thoroughly mixed, thus the diffusion distance may be ignored.)

Allometric Coefficients

The relationship of one variable with respect to another can be summarized by the allometric coefficient of the equation of the relationship. The value of this coefficient must be considered when determining whether a particular relationship exhibits isometric or allometric change. If a relationship is not isometric, the allometric coefficient will indicate which linear dimension increases at a faster rate than the other.

To obtain the allometric coefficient, we could express the first variable as a function of the second, using the general exponential equation:

$$y = \beta x^{\alpha}$$

In this equation, α (alpha) is the allometric coefficient relating the *x*-variable to the *y*-variable. The coefficient β (beta) is a constant. (There is a large and inconclusive body of literature dealing with the biological significance of the β coefficient, but we will not consider it in this laboratory.)

In Figure 4.1A, SA of a series of fictitious animals is expressed as an exponential function of VOL. You will note that we can also express the curvilinear (= curved line) relationship of VOL to SA by reversing the axes, as in Figure 4.1B, thereby expressing a different exponential equation. You will note that the allometric coefficients obtained, 0.6680 and 1.4945, are the inverse of each other.

The allometric coefficients can be obtained directly from the data by determining the exponential equation which best "fits" the data. However, this is difficult to obtain unless the logarithms (log_{10}) of the data are used. When using log-log plots of data, determining the allometric coefficients which relate two variables is quite simple.

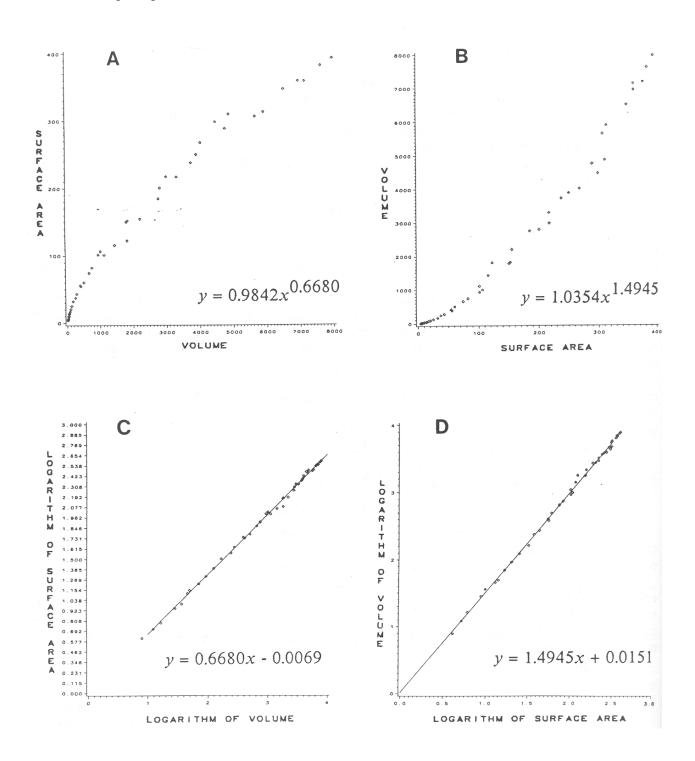
We have log-transformed and re-plotted the data on SA and VOL in Figures 4.1C and 4.1D; you will notice that the curvilinear relationships found in these plots are now linear—the relationships are described by straight lines, of the simple form:

$$\log_{10} y = \alpha \log_{10} x + \log_{10} \beta$$

The coefficients α and $\log_{10}\beta$ in this linear regression equation have the same values as the coefficients α and β in the exponential equation which described the raw data. In this linear equation, α , the slope of the line, is the allometric coefficient.

Typically, with real data from real organisms, the points do not cluster so tightly around either curved lines on raw data plots or straight lines on log–log transformed plots. This is to be expected, and calculating the α and β coefficients which define the "best" line through a relationship would be rather tedious without a computer program capable of determining regression equations.

Figure 4.1. Computer-generated plots illustrating the relationship between surface area (SA) and volume (VOL) for a series of fictitious animals; corresponding log-transformed relationships in plots C and D. See text for details.



Regression

Regression is a statistical procedure that allows you to find a line of best-fit to the data plotted as y versus x. You will use a computer program (*outside* of laboratory time) to identify lines of best-fit for the data collected in this laboratory. The results of this program will be used in your assignment. Instructions are provided in Appendix A.

About the Plots in Figure 4.1

The plots in Figure 4.1 were computer-generated and should not be used as examples when preparing the graphs in your assignment; see section 4.2 in *BIOMETRICS* (Goldman, 1987) for acceptable ways to graph quantitative data. Note that since the data are from a series of fictitious animals, no units are provided.

Determining if a Relationship is Isometric

Determining what the value of the **allometric coefficient** (α) would be if the relationship between two variables is **isometric** is done by comparing the **dimensional exponents** of the variables being compared. That is, are the variables linear dimensions such as *length* or *width* (dimensional exponent = 1), squares of linear dimensions such as *surface area* (dimensional exponent = 2), cubes of linear dimensions such as *volume* (dimensional exponent = 3), or, dimensionless such as *length/width* (dimensional exponent = 0)? (*Weight* is a three-dimensional measure and has a dimensional exponent of 3.)

The α -value that would be associated with an isometric relationship is determined by dividing the dimensional exponent of the *y*-variable by the dimensional exponent of the *x*-variable (i.e., y/x). A few examples will serve as an illustration.

If *length* and *width* are isometrically related, α will be 1 (i.e., 1/1). If *length* is isometrically related to *surface area*, α will be either 2 or 0.5 (depending on which dimension is plotted on which axis). If *length* is isometrically related to *volume*, α will be either 3 or 0.33. If *volume* is isometrically related to *surface area*, α will be either 1.5 or 0.67.

If the relationship of *length/width* and *height* is isometric, α will be either 0 or infinity. The dimensional exponent for a ratio (e.g., *length/surface area*) is calculated by *subtracting* the exponent of the numerator by the exponent of the denominator (e.g., 1 - 2 = -1).

If a morphometric relationship is **not isometric**, then α will have any value except the isometric one. The regression program described in Appendix A provides two ways to statistically test whether the relationship between morphometric variables is isometric or allometric; either of these methods will be used in your assignment.

Limitations of Allometry

Preparing an allometric plot and determining the relationship between the variables and the allometric coefficient do not in themselves *explain* the change in proportions; they merely show precisely that there is a change in proportions with a change in size. One cannot dogmatically answer the question, Why do such changes in proportions occur?, but one can set up interesting and reasonable hypotheses that are supported by the experimental data.

Part 1: Change in Shape Without Change in Volume

The first exercise illustrates how organisms can compensate for a reduction in SA:VOL by changing shape. To demonstrate the effect of changing shape alone, you will look at a series of acrylic shapes all of which have approximately the same volume. It is important to know how to calculate specific dimensions for simple shapes *before* you must do so for more complex shapes in Part 2.

Each student should measure the seven acrylic shapes and complete Table 4.2. Does it matter whether you measure the same face on the cube each time? The formulae for calculating SA and VOL for these shapes are in Appendix B. Before you proceed with Part 2, check with your instructor to be certain Table 4.2 is completed correctly.

The dimensions of the acrylic shapes you measured vary considerably. Although they appear unrelated in all respects, the volumes are approximately the same. This similarity is by intention to illustrate the interrelationship of volume and shape.

Table 4.2. Summary of measurements for seven acrylic geometric shapes.

SHAPE	Length (cm)	Width (cm)	Height (cm)	LxW (cm^2)	HxW (cm^2)	$SA (cm^2)$	VOL (cm³)	SA:VOL (cm ⁻¹)
Cube		XXX	XXX	XXX	XXX			
Short rectangular solid								
Long rectangular solid								

SHAPE	Outer Radius (R) (cm)	Inner Radius (R') (cm)	Length (cm)	SA (cm^2)	$VOL \ (cm^3)$	$SA:VOL$ (cm^{-1})
Short cylinder		xxx	(/		(***)	(***)
Long cylinder		XXX				
Pipe						
Sphere		XXX	XXX			

Part 2: Allometry Experiment

In the second exercise you will investigate how animals of different sizes change proportions to compensate for changes of SA and VOL. In particular, you will look at the allometry of total surface area (SA), total volume (VOL), minimum leg cross-sectional area (MLXA), and body size (SIZE) for a series of North American mammals.

But first, we should consider just what **size** is. We have defined allometry, but not size. Intuitively, size is a measure of how big something is. But what does "big" really mean? For instance, which individual would you consider larger: a linebacker on a football team or a forward on a basketball team? How might you decide? The problem comes down to how size is quantified. There are numerous possibilities, but no general agreement among biologists on either how size should be measured or even what size really is.

The greatest length of an organism has often been used to estimate overall size. This is fine when comparing flatworms with flatworms, but what about when comparing flatworms with humans, salamanders, locusts, clams, and swordfish? Some researchers have used volume, while others have used the cube root of volume. Others have used extremely complex mathematical models to derive imaginary "size" vectors. Recently, many researchers have simply taken an arbitrary number (though typically quite a large number) of arbitrary linear measurements on each animal, and have then taken the average of these measurements. Averages are then considered to be a measure of size and can be compared. What would you do? And how would you quantify shape in such a way that it is independent of size? (This is both a complex and current problem; a graduate student earned a Ph.D. from the University of Toronto for work on this very question.)

In this laboratory you are going to use the cube root of volume as a measure of size (hereby denoted as SIZE):

Objectives

Each student will be given one illustration of a North American mammal (20 different animals per room) and will calculate (with the aid of a computer program) an approximation of its (1) total surface area (SA), (2) total volume (VOL), (3) minimum leg cross-sectional area (MLXA), and (4) SIZE. You will be investigating the following:

- 1. The relationship between MLXA and SIZE: The strength of a leg bone depends upon the area of its minimum cross-section (MLXA), but the legs must support a body that increases in weight as the cube of its length. You will determine the relationship between MLXA and SIZE for the North American mammals examined in the laboratory. Does this relationship exhibit isometric or allometric change?
- 2. The relationship between SA:VOL and SIZE: As mentioned earlier, by growing larger the surface area of an object will continually decrease relative to its volume when its shape remains unchanged. You will determine the relationship between SA:VOL and SIZE for the North American mammals examined in the laboratory—ranging in size from a mouse to a bison. Does this relationship exhibit isometric or allometric change?

Procedures for Part 2

Using Figure 4.2 as a guide, you will notice that a quadruped (four-legged animal) can be summarized by eight body segments (head, neck, body, four legs, and tail). To keep things simple, each body segment will be summarized by only one geometric shape and you will be limited in the choice of shapes for each segment.

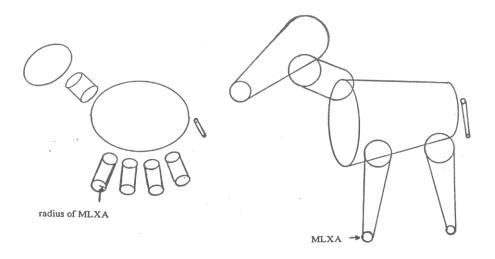


Figure 4.2. Typical quadrupeds summarized by various geometric shapes.

It is very important to study Appendix C (a detailed discussion on calculating SA and VOL for a quadruped) before proceeding to take measurements from your animal illustration. (It is also highly recommended that you prepare a protocol for this laboratory.) A summary of things to do is as follows:

1. Each student is to summarize SA and VOL, for one animal, as a combination of six body segments (it is assumed that both forelegs are the same shape as each other, and that the rear legs are the same as one another). Use whichever geometric shapes best approximate the specific animal you are working on. (For instance, simple cylinders may be appropriate for the legs of an elephant, but frustums may be more appropriate for the legs of an armadillo.) When calculating SAs, the computer program will not include surfaces which are not on the animals exterior, such as the proximal end of the leg-tubes and the equivalent areas where the leg-tubes would attach to the body. To keep things simple, you are restricted to the following geometric shapes (see Appendix B):

head: frustum, spheroid, sphere, cone, or cylinder

neck: frustum, cylinder, or absent body: frustum, spheroid, or cylinder

legs: frustum or cylinder tail: cone, cylinder, or absent

- 2. MLXA is calculated as the minimum cross-section of the smallest *leg* (not foot) taken *above* the ground (this would be just above the ankle in humans). Do *not* include feet. Assume that the leg is circular; MLXA is calculated as the area of a circle (see Figure 4.2). MLXA is measured in centimeters.
- 3. SIZE will be measured by the *computer* as the total length of the head, neck, and body.
- 4. At the end of the laboratory your instructor will enter class data in the computer to generate a table of all class values to be used in your assignment.

Computer-assisted Data Calculation

An interactive computer program will assist you in calculating several of the specific dimensions from your quadruped. You will be requested by the program to select which shapes approximate each body segment and then to supply the specific parameters for each shape (for example: for a circular frustum provide r_1 , r_2 , and H in decimeters). The program will list the values that you have provided and give you the opportunity to make corrections or alter your choice as to what shape best approximates a given body segment. The program will then draw your animal based on the specifications that you have provided. If you accept this drawing (i.e., dimensions and shapes are correct) you can request a summary which will include: Total SA, Total VOL, SIZE, MLXA, SA:VOL, and the logarithms (log_{10}) of SIZE, MLXA, and SA:VOL. Detailed instructions will be provided by your instructor.

Assignment

Objectives

In the format of a formal laboratory report, present the results of your investigations from Part 2. The marks assigned per section are as follows (total=150): Title and Introduction (20), Materials and Methods (5), Results (40), Discussion (70), and Conclusion (15). Your report *must not exceed 1000 words in length* (about four pages at 250 words per page; excluding tables, graphs, and literature cited) and should be double-spaced and, if possible, typed. It should address, but not be limited to, the following:

- 1. A *brief* synopsis of general materials and methods is all that is required in your Materials and Methods section; the details of the procedures for utilizing the computer programs should *not* be included.
- 2. Your Results section should include: the computerized-drawing of your animal illustration, the class data, computer printouts from the regression program, and two graphs (see 4 and 5 below). Remember to highlight/summarize *in writing* the significant aspects of your results.
- 3. The regression program (Appendix A) provides two ways to test for isometric versus allometric change (predicting the isometric slope and using the 95% confidence limits of the actual slope); *either* of these methods is acceptable.

- 4. On regular graph paper plot log(MLXA) vs. log(SIZE) for the mammals examined in the laboratory. Which variable should be plotted along the *x*-axis and which one along the *y*-axis? Indicate which animal is represented by each point on your graph. Discuss the relationship between MLXA and SIZE as indicated by the data. Does this relationship exhibit isometric or allometric change?
- 5. Prepare a similar plot of log(SA:VOL) vs. log(SIZE). Discuss the relationship between these two variables as indicated by the data. Does this relationship exhibit isometric or allometric change? Do smaller animals have greater or lesser SA:VOLs than larger animals? Generally speaking, how might this be related to the animal's lifestyle?

Literature Cited

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- McMahon, T. A., and J. T. Bonner. 1983. On size and life. Scientific American Books, New York, 255 pages.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, 329 pages.
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- Schmidt-Nielsen, K. 1975. Scaling in biology: The consequences of size. Journal of Experimental Zoology, 194:287–307.
- ———. 1984. Scaling: Why is animal size so important? Cambridge University Press, 241 pages. Smith, R. J. 1980. Rethinking allometry. Journal of Theoretical Biology, 87:97–111.
- Sweet, S. S. 1980. Allometric inference in morphology. American Zoologist, 20:643–652.

There is a large and growing body of literature pertaining to allometry. A computerized literature search in *Biological Abstracts* revealed 502 articles listed between 1985 and 1988 (4 years) that had *allometry* in the title or abstract, or as a key word. Calder (1984) listed over 600 references.

APPENDIX A Regression

Regression is a statistical procedure that allows you to find a line of best-fit to data plotted as *y* versus *x*. It is not the only procedure for fitting straight lines to data but is the most appropriate for the data you will be analyzing in this laboratory. You will use a computer program to identify lines of best-fit for the data collected in this laboratory. To use the program, just type the word REGRESSION and hit [Enter]. Instructions will appear on the screen.

An important reason for using regression is to test whether the relationship between morphometric variables is isometric or allometric. This relationship is usually described by the slope of the regression line on a plot of log-transformed data. In some cases it is possible to predict what the slope might be if the relationship is isometric. For example, if you plot log(SA) against log(VOL) for a series of spheres, you would expect the line to have a slope of 0.67. (Why would you expect this?)

The regression program provides two ways to test for isometric versus allometric change: predicting the isometric slope and using the 95% confidence limits of the actual slope.

Predicting the Isometric Slope of the Line

After you have entered your data into REGRESSION, the computer will ask you to enter your prediction for the isometric slope of the line. (If you do not have a prediction, just hit [Enter] and the predicted slope will be 0, which represents a horizontal line.) The computer will then perform a t test and determine whether the actual slope of the regression line is significantly different at probability levels of 0.01 or 0.05 to your predicted isometric slope. The null hypothesis is that the two slopes are not significantly different. (To perform the t test, the computer compares the y-values you actually enter with the y-values along the line of predicted slope.)

If you do predict the isometric slope, make sure you justify your prediction in your assignment. Why would you expect the slope to have that value?

95% Confidence Limits of the Slope

The second method of testing for isometric or allometric change is to look at the 95% confidence limits of the actual slope. These limits express how close your data are to the regression line. In the examples given in Figure 4.1, the data points all lie extremely close to the line. This is often true of data which have been log-transformed. However, the data in the graph below are a little more scattered. (Have they been log-transformed?) The solid line is the regression line, or line of best-fit. It does seem to follow the trend, but would you have drawn that particular line as a line of best-fit?

The two dashed lines represent the 95% confidence limits of the slope. They indicate that the slope of any line drawn between these two limits is not significantly different (P > 0.05) from the slope of the regression line.

You can use the 95% confidence limits of log-transformed data to test for isometry between your x- and y-variables. The computer will provide you with values for the slopes of the 95% confidence limits. You have to determine what the slope should be if the relationship between x and y is isometric. If this isometric slope falls between the upper and lower 95% confidence limits, then the regression slope and the isometric slope are not significantly different (P > 0.05). If the isometric slope lies outside the limits, then the slopes are significantly different (P < 0.05).

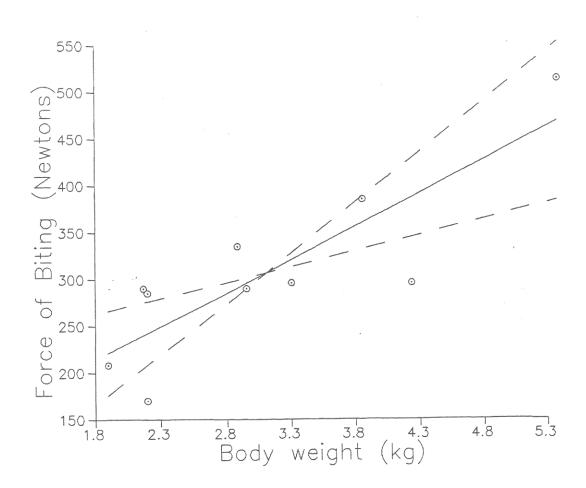


Figure 4.3. Plot of force of biting versus body weight.

Notice that the solid regression line and the two dashed lines all cross at a single point. This point is at the mean of both x and y sets of values (,), which will be useful to know if you choose to plot all three lines on the graphs in your assignment.

Interpreting the Printout of Results

When the computer has analyzed your data it will display a screen summarizing the results and give you the option of printing them. (A sample is provided in Figure 4.4.) The screen display and printout will give the mean and standard deviation of your x and y data sets and the number (N) of values in each set. The means may be of use when you are plotting your graphs. The correlation (r) is another way of determining how close the data points are to the line and indicates the strength of the bivariate relationship. It is included here for your interest.

In the middle of the screen are the important values: the slope of the regression line and the upper and lower 95% confidence limits of the slope. The corresponding intercepts on the *y*-axis are also given. Below these results is the summary of the *t* test of actual versus predicted slopes. It provides a way of determining whether the relationship between the variables is isometric. If you did not enter a prediction, the test slope is 0 (i.e., the slope of a horizontal line). The printout will also display your raw data.

Plotting your Graphs

You can use the data on the printout to help plot the regression line and 95% confidence limits.

- 1. Decide how you want to scale your axes. See the *BIOMETRICS* manual for hints. The program REGRESSION will display a graph after the Results screen, which should also help you scale the axes.
- 2. Mark the point on your graph with the coordinates $(\overline{x}, \overline{y})$, i.e., the mean x and y.
- 3. From this point, move in the x direction an appropriate distance, Δx . (What is an appropriate distance? As an example, in Figure 4.3 is 3.1, and the maximum value of x is 5.3; the difference between them is 2.2. So we might take Δx to be 2.0 because it is a round number which "fits" well on the graph.) Mark the point whose coordinates are ($x + \Delta x$,).
- 4. Move in the y direction a distance Δy which corresponds to Δx :

$$\Delta y = \alpha \times \Delta x$$

where α is the slope of the regression line. If Δy is positive move upwards, if Δy is negative move downwards, and mark the point ($x \mp \Delta x$, $y + \Delta y$).

- 5. You now have two points through which the regression line passes and can draw the line. It is always more accurate to draw a straight line through three points than through two, and you might want to use $(\bar{x} \Delta x, \bar{y} \Delta y)$. for a third point. (Select a new Δx that fits the scale.)
- 6. To plot the 95% confidence limits, repeat steps (1) to (5) using the slopes of the upper and lower 95% confidence limits for α .
- 7. An alternate method is to use the equation y = mx + b (m = slope); select a value for x to determine the value of y.

Figure 4.4. Printout from REGRESSION program.

Regression	of log(Vo	lume) on log(I	ength)	
Mean Standard De Correlation	viation	og(Length) 0.6716 0.3358 0.9953	log(Volume) 1.9729 0.9957	N 14
Slope Intercept	•••••	Best fit 2.9512 -0.0091	Upper 95% 3.1319 -0.1305	Lower 95% 2.7705 0.1122
Probability From table t(0.01), 1 t(0.05), 1	that the 2 df = 2 df =	3.0550 2.1790	ificantly different from calculation t = 0.5890 Therefore, P>0.10, No.	com 3.0
Raw Da	ta		Logarithms	
	Length (cm)	Volume (cm^3)	log(X)	log(Y)
	1.2000 2.4000 2.9000	1.1000 9.1000 26.2000	0.0792 0.3802 0.4624	0.0414 0.9590 1.4183
	4.0000 6.9000 7.6000 0.4000	62.5000 320.0000 331.8000 1003.3000	0.6021 0.8388 0.8808 1.0170	1.7959 2.5052 2.5209 3.0014
	8.3000 4.9000 0.9000	540.5000 137.6000 1.1000	0.9191 0.6902 -0.0458	2.7328 2.1386 0.0414
	9.5000 8.2000 6.4000 7.6000	729.0000 530.9000 215.7000 350.1000	0.9777 0.9138 0.8062 0.8808	2.8627 2.7250 2.3339 2.5442

APPENDIX B General Formulae for Calculating Areas and Volumes

By convention, unless specifically indicated otherwise, the basic dimensions used by morphologists for biological objects are:

Length (*L*): largest measurement

Width (W): next largest measurement perpendicular to L

Height (H): next largest measurement perpendicular to L and W

A typical exception in manufactured objects is a tower or building—the height of which is often the greatest measurement. Also, the height of pyramids and cones is the distance from vertex to base.

The following table provides formulae for calculating surface area (SA) and volume (VOL) for some of the various shapes you will use in this laboratory. Formulae for pipe, frustum, and spheroid are given on the next page. (Note: a frustum is a cone with the tip removed and its SA and VOL can be calculated similarly; however, a simpler technique is to provide one formula.)

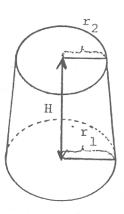
ectangle L^2 — ectangle LW — ectangular $2 \left(LW + LH + WH \right) LWH$ olid eube $6L^2$ L^3 ephere $4\pi r^2$ $\left(\frac{4}{3} \right) \pi r^3$ ene $\pi r \left(\sqrt{r^2 + H^2} + r \right) \pi r^2 \left(\frac{H}{3} \right)$	Shapes	SA	VOL
ectangle LW — ectangular $2 \left(LW + LH + WH \right) LWH$ olid sube $6L^2$ L^3 sphere $4\pi r^2$ $\left(\frac{4}{3} \right) \pi r^3$ cone $\pi r \left(\sqrt{r^2 + H^2} + r \right) \pi r^2 \left(\frac{H}{3} \right)$ explicitly $\pi r^2 L$	circle	πr^2	
ectangle LW — ectangular $2 \left(LW + LH + WH \right)$ LWH olid tube $6L^2$ L^3 sphere $4\pi r^2$ $\left(\frac{4}{3} \right) \pi r^3$ cone $\pi r \left(\sqrt{r^2 + H^2} + r \right)$ $\pi r^2 \left(\frac{H}{3} \right)$ eylinder $2\pi r \left(L + r \right)$ $\pi r^2 L$	ellipse	πab	-)
ectangular $2\left(LW + LH + WH\right)$ LWH olid sube $6L^{2}$ L^{3} $4\pi r^{2}$ $\frac{4}{3}\pi r^{3}$ sphere $\pi r \left(\sqrt{r^{2} + H^{2}} + r\right)$ $\pi r^{2} \left(\frac{H}{3}\right)$ evylinder $2\pi r \left(L + r\right)$ $\pi r^{2}L$ r (pronounced pie) = 3.1415927 (approximately!)	quare	L^2	
sphere $6L^2$ L^3 sphere $4\pi r^2$ $\left(\frac{4}{3}\right)\pi r^3$ sphere $\pi r \left(\sqrt{r^2 + H^2} + r\right)$ $\pi r^2 \left(\frac{H}{3}\right)$ sylinder $2\pi r \left(L + r\right)$ $\pi r^2 L$	ectangle	LW	2 <u>2</u> 3 25 <u>320110</u> 0 0
sphere $4\pi r^2$ $\left(\frac{4}{3}\right)\pi r^3$ sphere cone $\pi r \left(\sqrt{r^2 + H^2} + r\right) = \pi r^2 \left(\frac{H}{3}\right)$ cylinder $2\pi r \left(L + r\right) = \pi r^2 L$ r (pronounced pie) = 3.1415927 (approximately!)	rectangular solid	$2\left(LW + LH + WH\right)$	LWH
sphere $\pi r \left(\sqrt{r^2 + H^2} + r \right) = \pi r^2 \left(\frac{H}{3} \right)$ Eylinder $2\pi r \left(L + r \right) = \pi r^2 L$ $\pi \text{ (pronounced } pie \text{)} = 3.1415927 \text{ (approximately!)}$	cube	6L ²	L^3
Eylinder $2\pi r \left(L + r\right) = \pi r^2 L$ Tr (pronounced pie) = 3.1415927 (approximately!)	sphere	$4\pi r^2$	
r (pronounced pie) = 3.1415927 (approximately!)	cone	$\pi r \left[\sqrt{r^2 + H^2} + r \right]$	$\pi r^2 \left(\frac{H}{3}\right)$
	cylinder	$2\pi r \left(L + r\right)$	$\pi r^2 L$
	π (pronounced	1 pie) = 3.1415927 (ap	proximately!

Circular frustum:

$$SA = \pi \left[r_1 + r_2 \right] \sqrt{H^2 + (r_1 - r_2)^2} + \pi r_1^2 + \pi r_2^2$$

$$= \pi \left[\left[r_1 + r_2 \right] \sqrt{H^2 + (r_1 - r_2)^2} + r_1^2 + r_2^2 \right]$$

$$VOL = \pi \left[\frac{H}{3} \right] \left[r_1^2 + r_1 r_2 + r_2^2 \right]$$

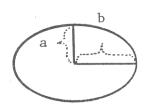


Prolate spheroid:

$$SA = 2 \pi b^{2} + \left[\frac{2 \pi a b}{z} \text{ arcsine } z\right]$$

$$z = \frac{\sqrt{b^{2} - a^{2}}}{b}$$

$$VOL = \left[\frac{4}{3}\right] \pi b a^{2}$$



NOTE: a = vertical axis; b = lengthwise axis. Calculate arcsine in radians. z is the eccentricity of the ellipse. A prolate spheroid is formed by the rotation of an ellipse around a major axis.

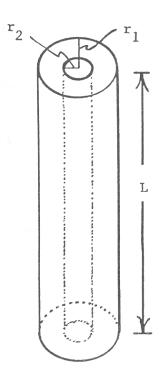
Pipe:

$$SA = \left[2 \pi r_1 L\right] + \left[2 \pi r_2 L\right] + 2\left[\pi r_1^2 - \pi r_2^2\right]$$

$$= 2 \pi \left[r_1 L + r_2 L + \left[r_1^2 - r_2^2\right]\right]$$

$$VOL = L \left[\pi r_1^2 - \pi r_2^2\right]$$

$$= L \pi \left[r_1^2 - r_2^2\right]$$



APPENDIX C Calculating SA and VOL of a Quadruped

NOTE: It is very important to thoroughly understand this appendix before proceeding with Part 2. Some of the text that follows is required in the event that the computer program is unavailable.

Step 1: Drawing Shapes

First, you must draw the geometric shapes to summarize each of the six body segments. Keep in mind the following:

- a) It should only be necessary to calculate one or two legs; if all legs are similar in shape calculate SA and VOL accordingly. Do *not* include ears, antlers, or horns.
- b) Some animals have tufts of fur about the head, bushy tails, etc. Do not include these in your calculations. Why? Estimate what the head would be like without the tuft of hair, the tail if it were not bushy, etc. Similarly, some animals have their legs bent, bodies in an arched position, etc. Consider these factors when estimating the specific dimensions of a shape and *alter* accordingly (i.e., straighten legs, body, etc.).
- c) For *some* animals it may be possible to include the neck with the geometric shape selected for the head or body; thus you would have only five shapes. Also, in some animals, the tail may be so small that SA and VOL will be insignificant; thus, the tail can be omitted.

Step 2: Recording Measurements

Once you have traced the geometric shapes, you are ready to take the necessary measurements. Study the formulae given in Appendix B to determine which measurements need to be recorded. Keep in mind the following:

- a) When calculating SA and VOL for all shapes you will be using radii and *not* diameters. Be careful and record only radii where they are required.
- b) Remember that you only want to measure SAs of exposed surfaces; for example, for the bison you would *not* want SA of the area between head and neck, neck and body, etc. (The computer program will do this for you!) This is mentioned here because it may influence which measurements you record. For example, in calculating SA for the bison neck, the areas in contact with the head and body are not desired. Therefore, the cylinder should be oriented so that it is short and wide (not long and narrow). In this way when SA is calculated (see formula) the areas of the two ends (contact areas: $2\pi r^2$) can be eliminated.
 - Before actually taking measurements with a metric ruler or calipers, there are two more important points to consider.
- c) For consistency, everyone must record their measurements in decimeters (1 dm = 10 cm = 100 mm). It is probably easiest to read the measurements from the picture in millimeters, then convert to decimeters (1 mm = 0.01 dm), and finally multiply by the scale factor (see below). (NOTE: the last two steps can be simplified to one.) If SA and VOL are calculated by hand, convert units to decimeters before squaring or cubing numbers.
- d) Should you calculate SAs and VOLs for the drawing or of the actual animal? Do you know the size of the actual animal? A **scale factor** is given on each drawing. For the bison it is 1:20.7, thus each measurement is multiplied by 20.7. Adjust for the scale factor before SA and VOL

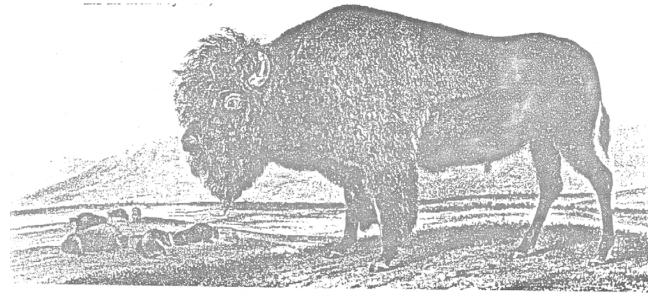
66 Allometry

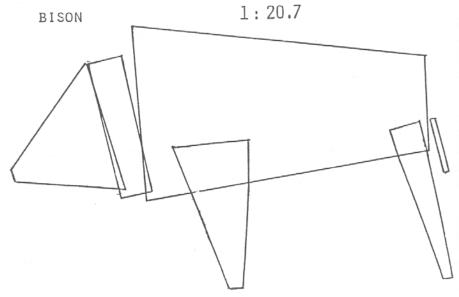
are calculated. (Remember that in many of the formulae some values are squared, and others are not.)

Step 3: Calculating SA and VOL

By now you should have a drawing with no more than six geometric shapes. For each shape you will have recorded the required measurements. For example, for a frustum you will have two radii and a height. You will need to do the following (parts omitted if computer program is used):

- a) Select the appropriate formulae from Appendix B. Be sure you know how to use them. *Check with your instructor* if the mathematics are unclear.
- b) To avoid calculation errors, write down the values as they are computed.
- c) Remember that when calculating SA do not include (if possible) areas which are not exposed. In the bison example $[\pi 4.04^2]$ would not be included in the SA formula for the head. NOTE: It may not be possible to subtract all of the unexposed areas from your calculations (e.g., if the head were a sphere and the neck a cylinder).





APPENDIX D Shareware Computer Programs

The shareware (user-supported) concept of marketing computer software differs from public-domain software and the standard marketing procedures for commercial software. The following is adapted from *Public Domain and Shareware* by Dan Marmion (Small Computers in Libraries, 7(11):4–9, 1987).

Commercial software is copyrighted, and may also be copy-protected, so that the user is legally constrained from making copies of it. The cost of commercial software is often expensive in order to recoup the costs of development and marketing, pay salaries of employees, and make a profit for the parent company.

Public-domain software, on the other hand, is neither copyrighted nor copy-protected, nor is it in any way commercial software. The authors of this type of software ask for no monetary compensation and simply release their programs into the public domain for anybody to copy and use.

Shareware is in between commercial and public-domain software and is based on the principle that the user should have a chance to use and evaluate a program before having to pay money for it. Shareware is not copy-protected, but it is copyrighted. A shareware product usually consists of an executable file and a documentation file. Users read the documentation to see how the program works, then use it until they are satisfied with the program and will continue to use it, or it is not what they want and will cease using it. If users like and expect to use the product, then they register it with the author by sending a fee. Payment of the registration fee acknowledges support of the shareware concept and encourages further development of user-supported software. Other benefits of registration may include a printed manual, telephone support, and notification of newer versions of the program. Shareware products can be obtained on disk for a nominal cost or downloaded from electronic bulletin boards.

Availability of Programs

The programs (CALCULATOR, CLASSDATA, and REGRESSION) that accompany this exercise are being made available as shareware. The disk(s) containing the executable files and documentation files can be obtained by sending a money order for \$10.00 US (\$12.00 CDN; includes floppy disks, disk mailer, handling, and postage; please specify disk size) to: Corey A. Goldman, University of Toronto, 25 Harbord Street, Toronto, Ontario, Canada M5S 1A1. Sample class data are also available.

User Support/Registration

If you find the programs of value and expect to use them, please register them by sending a fee to the above address (payable to UNIVERSITY OF TORONTO). The fee to register all three programs is \$75 US (\$90 CDN). (A registration form is provided in a file on the distribution disk.) Payment of the registration fee (1) ensures notification of newer versions of the programs and limited telephone support, (2) encourages further development of user-supported software, and (3) acknowledges support of the shareware concept.

BIOMETRICS Computer Program

BIOMETRICS is an interactive computer program written by Jeffrey J. Thomason and Corey A. Goldman to accompany the 32-page self-study manual used at the University of Toronto entitled "BIOMETRICS: an introduction to statistics and the scientific method" (Corey A. Goldman, Editor). The aim of the program is to give students practise solving problems involving the use of numbers and units. It is composed of five sections: significant figures, rounding numbers, converting units, scientific notation, and magnification. A copy of the self-study manual and/or computer program can be obtained by writing to the above address.

APPENDIX E

Problem to be Discussed at the Beginning of the Laboratory

A multicellular, spherical, aquatic organism has a central cavity containing water. It does not exchange oxygen with this central fluid. The radius of the entire organism is 2 cm, and the radius of the central cavity is 1.5 cm. This organism can obtain enough oxygen from the water surrounding it if the dissolved oxygen in the water equals 4 ml per liter. Could the same organism grow to have a radius of 4 cm if the oxygen concentration of the water were increased to 6 ml per liter? Consider what would happen both in a situation of isometric and allometric growth (that is, in one instance the layer of cells becomes 1 cm thick, while in the other the layer of cells remains 0.5 cm thick.) Give reasons for your answer and show all your calculations. (Consider only the external surface area and assume that the cytoplasm is thoroughly mixed, thus the diffusion distance may be ignored.)

Solution

The initial oxygen concentration is 4 ml/liter. The oxygen concentration increases by factor of 1.5 to 6 ml/liter. Thus the SA:VOL ratio can decrease from the initial value by a factor of 1.5. Organisms with new SA:VOL lower than this die, while those with SA:VOL equal to or higher than this value survive. Remember that only external SA is to be considered.

Initial organism

r = 2 cm layer of cells = 0.5 cm $SA = 50.3 \text{ cm}^2$ $VOL = 19.4 \text{ cm}^3$ $SA:VOL = 2.59 \text{ cm}^{-1}$

Thus, SA:VOL can decrease to 2.59/1.5 = 1.73 cm⁻¹

In isometric growth the animal dies since:

r = 4 cm layer of cells = 1 cm SA = 201.1 cm² VOL = 155.0 cm³ SA: VOL = 1.29 cm⁻¹

In allometric growth the animal survives since:

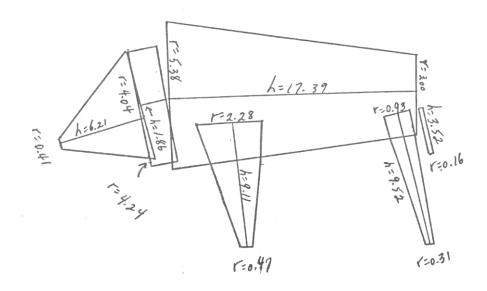
r = 4 cm layer of cells = 0.5 cm SA = 201.1 cm² VOL = 88.4 cm³ SA:VOL = 2.27 cm⁻¹

APPENDIX F Values for Acrylic Geometric Shapes Used in Part 1

SHAPE	Length (cm)	Width (cm)	Height (cm)	$L\times W$ (cm^2)	$L \times H$ (cm^2)	$H \times W$ (cm^2)	SA (cm²)	VOL (cm³)	SA:VOL (cm ⁻¹)
Cube	2.55	xxx	xxx	xxx	XXX	XXX	39.02	16.58	2.35
Short rectangular solid	5.06	2.51	1.12	12.70	5.67	2.81	42.36	14.22	2.98
Long rectangular solid	13.92	1.975	0.60	27.49	8.35	1.18	74.04	16.50	4.49

SHAPE	Outer Radius (R) (cm)	Inner Radius (R') (cm)	Length (cm)	SA (cm²)	VOL (cm³)	SA:VOL
Short cylinder	1.28	XXX	2.885	33.49	14.85	2.26
Long cylinder	0.66	XXX	13.98	60.76	19.13	3.18
Pipe	0.64	0.34	17.60	110.22	16.26	6.78
Sphere	1.58	XXX	XXX	31.37	16.52	1.90

APPENDIX G Data for Computer Demonstration on CALCULATOR Program

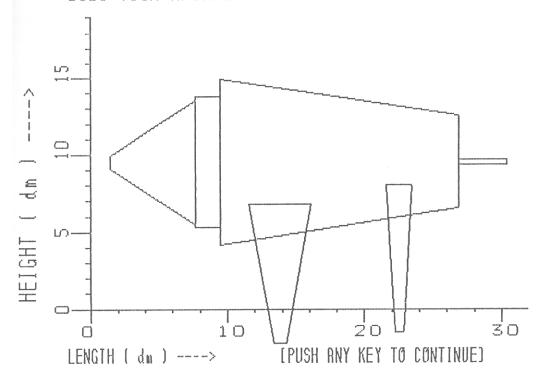


Actual measurements of bison (in dm) (note that illustration is reduced—original size as in Appendix C)

```
ENTER THE FOLLOWING VALUES:
HEAD: RADIUS of ANTERIOR end ( dm ) ? 0.41
HEAD: RADIUS of POSTERIOR end ( dm ) ? 4.04
HEAD: LENGTH ( dm ) ? 6.21
NECK: RADIUS ( dm ) ? 4.24
NECK: LENGTH ( dm ) ? 1.86
BODY: RADIUS of end attached to NECK ( dm ) ? 5.38
BODY: RADIUS of POSTERIOR END ( dm ) ? 3.00
BODY: LENGTH ( dm ) ? 17.39
FORELEG: RADIUS of end attached to BODY ( dm ) ? 2.28
FORELEG: RADIUS of end on the GROUND ( dm ) ? 0.47
FORELEG: LENGTH ( dm ) ? 9.11
HINDLEG: RADIUS of end attached to BODY ( dm ) ? 0.93
HINDLEG: RADIUS of end on the GROUND ( dm ) ? 0.31
HINDLEG: LENGTH ( dm ) ? 9.52
TAIL: RADIUS ( dm ) ? 0.16
TAIL: LENGTH ( dm ) ? 3.52
```

APPENDIX H Sample Output from CALCULATOR Computer Program

DOES YOUR ANIMAL LOOK ANYTHING LIKE THIS ?



RESULTS

Total SA is 872.5 dm2

Total VOL is 1357. dm3

SA/VOL ratio (SA:VOL) is .6430 dm-1

SIZE (Head + Neck + Body Length) is 254.6 cm

MLXA is 30.19 cm2

LOG10 of SIZE is 2.406

LOG10 of MLXA is 1.480

LOG10 of SA/VOL ratio (SA:VOL) is -.1918

^{***} REMEMBER ALL VALUES ARE CALCULATED USING RADII OF SHAPES ***