The purpose of this lab is to give you practice in translating and using formal models of biological phenomena, expressed in the form of equations.

Quantitative descriptions of biological phenomena permit one to calculate outcomes of interest, whether these be the clearance rate of a drug from the blood, or the production of wheat in a dry year. Calculations follow a recipe or algorithm that often is written in the compact form of a symbolic expression, or equation. The ability to carry out quantitative work in biology, as in the other natural sciences, depends on facility in translating and using symbolic expressions such as equations.

A second motivation, apart from the practical ability to carry out calculations, is that important ideas in some areas of biology are expressed in symbolic form, typically as equations or diagrams. The ability to understand these ideas depends upon the ability to translate abstract equations into concrete terms. For example, Kleiber's Law states that metabolic rate varies with body mass according to the following relation:

$$\dot{E} = \alpha M^{\beta}$$

where \dot{E} is metabolic rate at rest, M is mass of an animal, α is a parameter with units that scale metabolic rate to body mass, and β is a unitless parameter slightly greater than a theoretical value of 2/3 based on the ratio of surface area (Length²) to volume (Length³). Remember that parameters hold constant in a situation, they are conventionally expressed with Greek symbols, and they are often estimated from data by statistical methods. In contrast, the variable quantities \dot{E} and M can take on any of several values. With this information we can now state Kleiber's Law in more concrete terms:



"The metabolic rate \dot{E} of an animal at rest is directly proportional to its biomass M, raised to a power slightly greater than 2/3." (2/3 is the surface to volume ratio).

For passerine (perching) birds, Lasiewski and Dawson (1967, *Condor* 69:13) estimated that $\alpha = 129$ kcal day⁻¹ kg^{-0.724}, and that $\beta = 0.724$, a pure number with no units or dimensions.

Now re-write the equation with these parameter values

With this equation, you should now be able to calculate the minimum food energy requirement (in kilocalories per day) of a 20 gram (0.02 kg) canary.

 \dot{E} (0.02 kg) = _____ kcal/day Try stating this result in words.

The conventional way of reading $\dot{E}(0.02 \text{ kg})$ is "metabolic rate at two hundredths of a kilogram."

Now pick several reasonable values of the explanatory quantity (avian mass in kg), and make calculations of minimum (resting) metabolic rates.

Ė(_kg) =	kcal/day	Ė(_kg) =	kcal/day
Ė(_kg) =	kcal/day	Ė(kg) =	kcal/day

Everyone should do at least two of these on their own calculator, to become familiar with the mechanics. It also helps to state one of these calculations in verbal form, as a complete sentence. For example:

"The expected metabolic rate of a _____ gram bird, based on Laseiwski and Dawson's equation, is kcal per day."

The parameter values in this example are by no means unique. Other values are possible. For example Laseiwski and Dawson (1967) also estimated α and β for non-passerine birds. Try substituting their estimates ($\alpha = 78.3$ kcal day⁻¹ kg^{-0.723}. $\beta = 0.723$) to obtain an equation to calculate resting metabolic rate of a non-passerine bird from body mass, according to Kleiber's Law.

Ė = _____

Compare this equation (or model) to that for passerines. Which will have the greater metabolic rate, a passerine bird, or a non-passerine of the same mass?

Now check your guess by calculating the resting metabolic rate of a 20 gram non-passerine, and comparing it to the calculated rate for a passerine of the same mass.

 $\dot{E}(0.02 \text{ kg}) =$ _____ kcal/day Try stating this result in words.

The parameter α in Kleiber's Law has units, as do many of the parameters used in biology. Parameters should be stated with their units, because otherwise it is all too easy to write equations leading to erroneous calculations. For example, if a physiologist reports an estimate of $\alpha = 619$ for passerine birds, and fails to report the units, then it is natural to assume that this refers to kilocalories, which is incorrect. If we assume the physiologist meant kilocalories (for failure to report units) then our calculation will be far too high.

Try writing Kleiber's Law for $\alpha = 619$, then calculate the metabolic rate for the 20 gram sparrow.

 $\dot{E}(0.02 \text{ kg}) =$ _____ (kcal/day?)

This calculation is ______times higher than the rate for a resting passerine.

Failure to report units ($\alpha = 619$ kilojoule day⁻¹ kg^{-0.724}) led to this error.

Try calculating the metabolic rate (in kilojoules per day) of a 20 gram passerine (a sparrow) and a 500 gram passerine (a crow).

 $\dot{E}(0.02 \text{ kg}) =$ _____ kJ/day $\dot{E}(0.5 \text{ kg}) =$ _____ kJ/day

Based on this example, here is a generic recipe for translating and using equations:

Table 2.1. Calculations from equations expressing biological ideas.

- 1. Write the equation in symbolic form (symbols only).
- 2. Define each symbol in words and state units (if any).
- 3. State in words the idea expressed by the equation.
- 4. Write out parameter estimates and then write the equation with the parameter estimates. Sometimes these values are obtained from theory but more often they are obtained by estimation procedures such as least squares regression.
- 5. Show that units of all terms are equal.
- 6. Substitute specific values of variable quantities to calculate the quantity of interest from the equation.



For this lab, you will be given 3 examples from publications that use formal models (equations) to express biological concepts. In each example (tamarin behaviour, *Notonecta* allometry, helminth infection of snails) one equation has been circled. For each equation, provide a complete translation and calculation, following the 6 steps listed in the Table above.

You are encouraged to work in groups, discussing your answers.

Example 1 Tamarin behaviour.

In a study of maternal behaviour of 12 red-bellied tamarins, estradiol was the most abundant urinary estrogen during late pregnancy. Infant survival was used to divide this group into good and poor mothers as follows (p. 721 of article).



"In the group of females who were subsequently defined as good mothers, five out of six had two surviving infants after one week, including two mothers without sibling infant care experience; a third good mother without experience had one surviving infant. In the group defined as poor mothers, two mothers with sibling infant care experience had one surviving infant, and all other mothers had no surviving infants at the end of the first week; 10 out of 13 infants of poor mothers died at day 0."

Figure 1 from the article is shown below. The figure displays the mean concentrations of urinary estradiol during the last 35 days of gestation in good and poor mothers.

Calculate the expected estradiol level in poor mothers 33 days before birth, using the linear equation shown in Figure 1B.

Is this model any good? (Hint: consider whether the calculated value would be consistently too high or too low, depending on the number of days before birth).

Complete Table 2.1 for the Tamarin mothers.



FIG. 1. Changes in the urinary concentration (mean + confidence limits) of total estradiol during late pregnancy in red-bellied tamarins defined as (A) good and (B) poor mothers. Values are expressed as the antilog of the mean of transformed data and, for clarity, only the upper 95% confidence limit is shown. Means were calculated from all samples collected from each type of mother within each two-day period. Unless otherwise stated, the prepartum data in both (A) and (B) are for 6 females; the postpartum data are for 3 females. The relationship between urinary estradiol (Y) and time prior to birth (X) in each type of mother has been estimated by linear least-means square regression; the solid line is for the regression equation [good mothers: F(1,91)=0.20, p>0.65; poor mothers: F(1,96)=39.35, p<0.0001 (23)], a=p<0.05 versus day -35, -33, -31, -29 (Duncan's Multiple Range Test).

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Example 2. Notonecta allometry.

In example 104 from Simpson et al. (1960) the exponent α is called the coefficient of allometry (Greek *allo* = "other" and *metron* = "measure"). These coefficients describe the degree to which a part of the body remains in direct proportion to the total length as length changes. Synthlipsis to vertex is a measure of head length in the water bug *Notonecta*.



the average values of 37 females and 35 males of Notonecta undulata. In each case, X is total body length and Y is the measurement listed in the table. (Data from Clark and Hersh, 1939)							
	FEN	IALES	MALES				
	b	œ	Ь	α			
Body width	0.616	0.810	0.656	0.765			
Head width	0.445	0.790	0.482	0.742			
Synthlipsis to vertex	1.039	-0.271	1.020	0.262			
First leg	0.422	1.074	0.470	1.013			
Second leg	0.549	1.069	0.605	1.012			
Third leg	1.100	0.948	1.178	0.908			
Femur 1	0.153	1.066	0.188	0.971			
Femur 2	0.190	1.114	0.209	1.060			
Femur 3	0.268	1.141	0.286	1.104			
Tibia 1	0.140	1.144	0.152	1.101			
Tibia 2	0.209	1.059	0.223	1.013			
Tibia 3	0.348	0.964	0.373	0.924			
Tarsus I	0.119	1.028	0.138	0.945			
Tarsus 2	0.143	1.056	0.150	1.010			
Tarsus 3	0.517	0.742	0.503	0.743			

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Which parts of *Notonecta* have allometry coefficients close to 1? (These parts of the body remain in proportion as the animal grows)



Which parts of *Notonecta* have positive coefficients well below 1? (These parts change in proportion to body length, such that the <u>relative</u> size of the part becomes smaller in larger specimens).



Reprinted from G.G. Simpson, A. Roe, R.C. Lewontin. 1960. Quantitative Zoology. © Harcourt Brace & World, New York.

Which parts of *Notonecta* have negative coefficients of allometry? (The <u>absolute</u> size of this part becomes smaller in larger specimens)

Write an equation for body width of male *Notonecta undulata*.

Calculate the expected body width of a 4 mm and an 8 mm long male, and express this as the ratio of the expected ratio of body width to body length.

 Width(4 mm) = _____
 Width(4mm) / 4mm = _____

 Width(8 mm) = _____
 Width(8mm) / 8mm = _____

The table (called Example 104) shows the parameter estimates 15 allometric equation for female *Notonecta* and 15 allometric equations for male *Notonecta*. Complete Table 2.1 for <u>one</u> of these 30 allometric equations.

Example 3 Helminth infection of snails.

Anderson and May (1979 *Parasitology* 79: 63-94) developed a model that predicts prevalence of infection in areas where schistosomiasis is endemic, in the sense that the average human worm burden is greater than or of the order of unity. Prevalence of infection, defined as the equilibrium fraction of snails observed to be releasing cercariae, y^* , will be

$$y^* = f / [f + (1 - f) (\mu'' / \mu')].$$
(1a)

They define f, the % change in population number as

$$f = e^{-\mu \tau} \tag{1b}$$

From data discussed in preceding sections they suggest that the death rate of infected snails during the latent period of infection (μ ') is approximately equal to the death rate of uninfected snails infected snails not releasing cercariae (μ). If this is assumed to be true, equation (1) reduces to

$$y^* = f / [f + (1 - f) (\mu'' / \mu)].$$
(2a)

with

$$f = e^{-\mu \tau}$$

They present empirical estimates of the parameters μ (death rate of uninfected snails and infected snails not releasing cercariae), μ'' (death rate of snails shedding cercariae) and τ (pre-patent period of infection) in Tables 4, 5, and 6. For example, *S. mansoni* has a pre-patent period (τ) of approximately 5 weeks at 25 °C (Fig. 4a) and, in St Lucia, Sturrock & Webbe (1971) estimated the mortality rates μ and μ'' to be roughly 0.15 and 0.61/snail/week, respectively. [note: the correct units are (snail/snail) week⁻¹]. The insertion of the parameter values into equation (2a) yields the prediction that the equilibrium fraction of snails shedding cercariae (prevalence of infection) is approximately 18%. Anderson and May note that this estimate is slightly higher than the observed prevalence figures listed in their Table 1, but it is a considerable improvement over the predictions of conventional Macdonald-Nasell-Hirsch models.

What units does μ have?





(2b)

First, check the calculation from Anderson and May (1979).

Next, examine Table 4 from Anderson and May (1979) to determine what happens to latent period (τ) with change in temperature.

is material has been copied under license from CanCopy. esale or further copying of this material is strictly prohibited.	Table 4. Latent period (τ) from point of infection to release of cercariae: Schistosoma mansoni					
	Snail species	Tem- perature (°C)	Latent period (7) (days)	Author(s)		
	Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata Biomphalaria glabrata	21-24 23-25 26-28 31-33 23-24 25-28 28-30 18 32 22-28 nderson an ress.	42 30-37 22-23 18 31-38 25-45 28-35 55 17 21-35 d R.M. N	Pan (1965) Stirewalt (1954) Stirewalt (1954) Stirewalt (1954) Evans & Stirewalt (1951) Standen (1949) Schreiber & Schubert (1949) Sturrock & Webbe (1971) Sturrock & Webbe (1971) Sturrock & Sturrock (1970) May. 1979. Parasitology 79:63-94. ©		
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What happens to latent period τ as temperature decreases?

What happens to the survival *f* as latent period changes due to decrease in temperature?

At a guess, will this increase or decrease the equilibrium fraction y*?

Calculate a prediction for equilibrium fraction of snails shedding cercariae at 18 °C, based on information in Table 4.

Did decrease in temperature increase or decrease the predicted prevalence of infection?

Complete Table 2.1 for the helminth infection example.

Write-up.

Lab 2a. Each individual is responsible for turning in a lab report, which consists of 3 group presentations (steps 1-6) and one individual presentation as follows.

Lab 2b. After you have completed these 3 examples (all 6 steps), find another example in the published scientific literature, of an equation with at least two variables and two parameters. Parameters will usually be shown as parameter estimates, rather than symbols. Publications can be found on the course website.

http://www.mun.ca/biology/schneider/b4605/Data/

State the full reference for the equation (authors, title, journal name with volume and page number). Provide a complete translation and calculation by completing steps 1-6 in Table 2.1.

If you use an equation from a publication not on course website, and you want extra credit, be sure to write this on your lab report.