UMAP

Modules in Undergraduate Mathematics and Its Applications

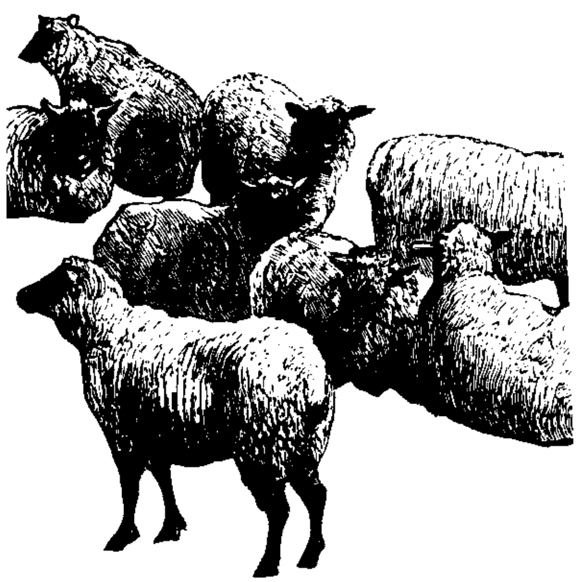
Published in cooperation with the Society for Industrial and Applied Mathematics, the Mathematical Association of America, the National Council of Teachers of Mathematics, the American Mathematical Association of Two-Year Colleges, The Institute of Management Sciences, and the American Statistical Association.

COMAP

Module 69

The Digestive Process of Sheep

Brindell Horelick
Sinan Koont



Applications of Biological Calculus

COMAP, Inc., Suite 210, 57 Bedford Street, Lexington, MA 02173 (617) 862-7878

Intermodular Description Sheet: UMAP Unit 69

Title: The Digestive Process of Sheep

Authors: Brindell Horelick and Sinan Koont
Dept. of Mathematics, University of Maryland, Baltimore, MD 21228
Dept. of Economics, University of Massachusetts, Amherst, MA 01003

Review Stage/Date: IV 7/30/80

Math Field: Calculus

Application Field: Biology

Target Audience: Second semester calculus students.

Abstract: This unit introduces a differential equations model for the digestive processes of sheep. Students describe the digestive processes of ruminants, explain how the assumptions of the model are translated into equations, discuss what support there is for the validity of the model, and discuss some possible conclusions to be drawn from the model.

Prerequisites: Know the properties of the exponential function (including $\lim e^{-t}$ as $t \to \infty$). Be able to determine the signs of $f'(t)$ and $f''(t)$ from a simple formula for $f(t)$, and be able to use this knowledge to graph $f(t)$ and find its maximum

$$\int_0^t \frac{r'(t)}{r(t)}\,dt\ .$$

THE DIGESTIVE PROCESS OF SHEEP

by

Brindell Horelick
Department of Mathematics
University of Maryland Baltimore County
Baltimore, Maryland 21228

and

Sinan Koont
Department of Economics
University of Massachusetts
Amherst, Massachusetts 01003

TABLE OF CONTENTS

Modules and Monographs in Undergraduate Mathematics and Its Applications (UMAP) Project

The goal of UMAP was to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and is now supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a non-profit corporation engaged in research and development in mathematics education.

The Project would like to thank Erwin Eltze of Fort Hays State University, Brian J. Winkel of Albion College, and John T. Annulis of University of Arkansas for their reviews, and all others who assisted in the production of this unit.

This unit was field-tested and/or student reviewed in preliminary form by Umesh Nargaratte of Medgar Evers College (CUNY), and Erwin Eltze of Fort Hays State University, and has been revised on the basis of data received from these sites.

This material was prepared with the support of National Science Foundation Grants No. SED 76-19615 AO2 and No. SPE-8304192. Recommendations expressed are those of the author and do not necessarily reflect the views of the NSF or of COMAP.

1. THE PROBLEM

There are various reasons why scientists are interested in studying the digestive processes of sheep. For example, these processes may shed light on the nutritional value of various feeding schedules or various methods of preparing food (such as coarse or fine grinding).

1.1 Description of the Digestive Process

A sheep is a *ruminant*; that is, a cud-chewing animal. Ruminants process their food as follows: eaten but unchewed food goes to a series of storage stomachs called the *rumen* and the *reticulum*. From there, after being chewed, it goes to the two digestive stomachs, the *psalterium* and the *abomasum*, and then to the *duodenum* (the first segment of the small intestine). Figure 1 is a simplified schematic of this process.

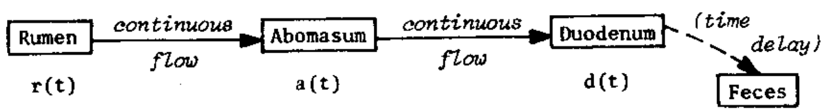


Figure 1. Schematic diagram of digestive process of sheep.

In due time, the food is discharged from the rectum in the form of feces. It is known that the flows from rumen to abomasum and from abomasum to duodenum are continuous. On the other hand, the discharge of feces is not continuous.

1.2 The Experiment

The parts of this process most readily observable are the very beginning and the very end. We can observe, and even control, what goes in the sheep and when it goes in. We can observe what comes out, and when. In practice, scientists (cf. Blaxter, Graham, & Wainman) feed sheep a certain type of food in carefully controlled amounts at carefully controlled time intervals. The food contains stained particles. By observing when the stained particles appear in the feces, the scientists can determine the length of time from consumption of the food to its excretion.

1.3 The Data

Data from a series of such experiments are shown in Figure 2. To analyze these data and learn something from them about the digestive processes we have outlined, we must find a concise and reasonably simple way to describe the data. In this article, we shall recount how some scientists have used calculus to develop such a description.

2. THE MODEL

2.1 The Functions $r(t)$, $a(t)$, and $d(t)$

Suppose that at time $t = 0$ a sheep is fed an amount R of food which goes immediately into its rumen. This food will pass gradually from the rumen through the abomasum into the duodenum. At any later time t we shall define

$r(t)$ = the amount of food still in the rumen;
$a(t)$ = the amount in the abomasum;
$d(t)$ = the amount which by then has arrived in the duodenum.

So $r(0) = R$, $a(0) = d(0) = 0$, and, for all $t > 0$,

$$r(t) + a(t) + d(t) = R. \tag{1}$$

(BE CAREFUL: $d(t)$ is not necessarily the amount of food *in* the duodenum at time t; some of it may have been excreted.)

2.2 The Assumptions

We shall make what appear to be two rather arbitrary assumptions.

(A) Food moves out of the rumen at a rate proportional to the amount of food in the rumen. Mathematically this says

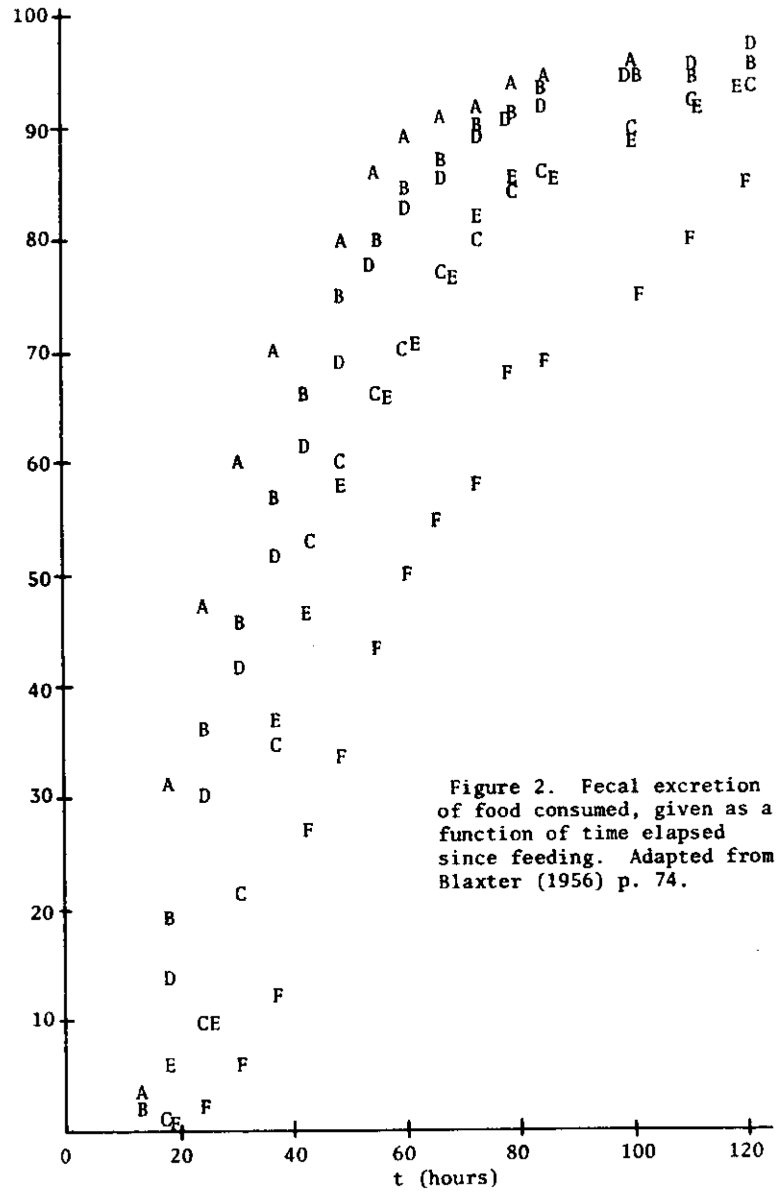


Figure 2. Fecal excretion of food consumed, given as a function of time elapsed since feeding. Adapted from Blaxter (1956) p. 74.

A: 1500 g finely ground and cubed dried grass
B: 1200 g " " " " " "
C: 600 g " " " " " "
D: 1500 g medium " " " " "
E: 1200 g " " " " " "
F: 600 g " " " " " "

(2) $$r'(t) = -k_1 r(t)$$

where k_1 is a positive proportionality constant.

(B) Food moves out of the abomasum at a rate proportional to the amount of food in the abomasum. Since at the same time food is moving into the abomasum at the rate given by Equation (2), the assumption says

(3) $$a'(t) = k_1 r(t) - k_2 a(t)$$

where k_2 is another positive proportionality constant.

3. THE SOLUTIONS OF THE EQUATIONS

3.1 Solving for r(t)

It is fairly straightforward to solve Equation (2) for r(t). We just divide through by r(t) and then integrate from 0 to t:

$$\int_0^t \frac{r'(t)}{r(t)}\,dt = -\int_0^t k_1 dt$$

$$\ln\left(\frac{r(t)}{R}\right) = -k_1 t,$$

since $r(0) = R$, and finally

(4) $$r(t) = Re^{-k_1 t}.$$

3.2 Solving for a(t)

Finding a(t) is a bit more tricky. Applying Equation (4) to Equation (3) we get

(5) $$a'(t) = k_1 Re^{-k_1 t} - k_2 a(t).$$

Equation (5) probably looks quite different from any you have seen before. Let us try to make a shrewd guess what kind of a solution it has. It says that the derivative of a(t) is the sum of two terms, $k_1 Re^{-k_1 t}$ and $-k_2 a(t)$. With luck, this might remind us of the product rule:

(6) $\quad$ if $a(t) = u(t) \cdot v(t)$

$$\text{then } a'(t) = u(t) \cdot v'(t) + v(t) \cdot u'(t).$$

Can we pick $u(t)$ and $v(t)$ so the terms in Equation (6) match up with the terms in Equation (5)? In other words, can we pick $u(t)$ and $v(t)$ so that

(7) $$u(t) \cdot v'(t) = k_1Re^{-k_1t}$$

and

(8) $$v(t) \cdot u'(t) = -k_2a(t)?$$

Since $a(t) = u(t) \cdot v(t)$, Equation (8) can be rewritten

$$v(t) \cdot u'(t) = -k_2u(t)v(t),$$

we are in business! The $v(t)$ factors cancel out, leaving us with

$$u'(t) = -k_2u(t)$$

which looks very much like Equation (2) and can be solved in the same way.

$$\int_0^t \frac{u'(t)}{u(t)}\,dt = -\int_0^t k_2dt.$$

Writing $K = u(0)$:

$$\ln\left(\frac{u(t)}{K}\right) = -k_2t$$

$$u(t) = Ke^{-k_2t}.$$

Putting this into Equation (7) gives

$$Ke^{-k_2t}v'(t) = k_1Re^{-k_1t}$$

$$v'(t) = \frac{k_1R}{K}\,e^{(k_2-k_1)t}.$$

If $k_1 = k_2$ we feel confident you can complete this solution yourself (Exercise 1).

Exercise 1. Find $a(t)$ if $k_1 = k_2$.

If $k_1 \neq k_2$, then $k_2 - k_1 \neq 0$ and so we can write

$$v(t) = \frac{k_1 R}{K(k_2-k_1)} e^{(k_2-k_1)t} + C$$

where C is the constant of integration. Then

$$a(t) = u(t) \cdot v(t) = \frac{k_1 R}{k_2-k_1} e^{-k_1 t} + CKe^{-k_2 t}.$$

Using the fact that $a(0) = 0$, we get

$$0 = \frac{k_1 R}{k_2-k_1} + CK$$

$$CK = -\frac{k_1 R}{k_2-k_1}$$

$$(9) \qquad a(t) = \frac{k_1 R}{k_2-k_1} (e^{-k_1 t} - e^{-k_2 t}).$$

Exercise 2. (a) Find the time t at which a(t) is maximum.

(b) Find the maximum value of a(t).

Exercise 3. If $k_1 = 2$ and $k_2 = 1$, how much food must the abomasum be able to hold if a meal of amount R is fed at time $t = 0$?

---

4. COMPARISON OF THE MODEL'S PREDICTIONS WITH THE EXPERIMENTAL DATA

So far, these results (Equations (4) and (9)) are purely theoretical and are, in fact, based on some rather arbitrary assumptions. To determine whether they are worth anything (let alone learn anything from them) we must see if they agree with the experimental data. And since the data concern fecal excretion as a function of time, we must first translate our results into results on fecal excretion.

4.1 Solving for d(t)

Starting with Equation (1), and using Equations (4) and (9) (still assuming $k_1 \neq k_2$):

$$d(t) = R - r(t) - a(t)$$

$$= R - Re^{-k_1 t} - \frac{k_1 R}{k_2 - k_1}(e^{-k_1 t} - e^{-k_2 t})$$

$$= R - \frac{R}{k_2 - k_1}(k_2 e^{-k_1 t} - k_1 e^{-k_2 t}).$$

4.2 The Formula for the Amount of Feces

Recall that $d(t)$ is the total amount of food which has entered the duodenum by time t, including food already excreted. Since excretion is not a continuous process, we cannot hope to represent it by an equation involving derivatives. Instead, we simply note that all food arriving in the duodenum is excreted after a certain time delay. Let us suppose that the average time delay is T hours. In other words, the amount of feces produced by any time $t > T$ is, on the average, the amount of food which had already entered the duodenum T hours earlier, at time $t - T$. If $f(t)$ denotes the amount of feces produced by time t, this says

$$f(t) = d(t-T) \text{ for all } t > T$$

$$f(t) = R - \frac{R}{k_2 - k_1}(k_2 e^{-k_1(t-T)} - k_1 e^{-k_2(t-T)}) \quad \text{for all } t > T. \tag{10}$$

Exercise 4.

(a) Determine the values of t for which $r'(t)$ is, respectively, positive, negative, and zero.

(b) Determine the values of t for which $r''(t)$ is, respectively, positive, negative, and zero.

(c) Determine $\lim_{t\to\infty} r(t)$.

Exercise 5. For the function $a(t)$ follow the instructions of Exercise 4.

Exercise 6. For the function $d(t)$ follow the instructions of Exercise 4.

Exercise 7. For the function $f(t)$ follow the instructions of Exercise 4.

Exercise 8. Use all the information in Exercises 4, 5, 6, and 7 to sketch the graphs of r, a, d, and f. You should *not* have to compute any points except r(0), a(0), d(0), and f(T), which you already know.

4.3 Least Squares Fit

Now what does it mean to say Equation (10) "agrees with" the experimental data? The equation contains three undetermined constants; k_1, k_2, and T. Each choice of the ordered triple (k_1, k_2, T) will result in a different curve. Some of these curves will "fit" the experimental data (that is, pass through or near the data points) better than others.

Any experimenter attempting to fit a theoretical curve with undetermined constants to his data must decide upon some criterion for determining how good a fit is, and whether one fit is better than another. Any criterion he chooses will have something to do with the distance of his data points from the curve, but not necessarily the shortest (perpendicular) distance. For example, an experimenter attempting to fit a curve to a succession of time-dependent observations may be interested in how well this curve predicts results for specified times. In that case he would be interested in how much each of his observations differs from the theoretically predicted value at the same time. In graphical terms, assuming time is measured on the horizontal axis, he is interested in the vertical distances from his data points to the theoretical curve. (See Figure 3 where, for simplicity, we have taken the theoretical curve to be a straight line.)

Several criteria of goodness of fit could be based upon these distances. The most common one is obtained by computing the sum of their squares. Squaring the distances assures that all the errors will appear as positive numbers, and so will not cancel each other out. It also magnifies the effect of relatively large errors, so one data point far from the curve will have more effect than several data

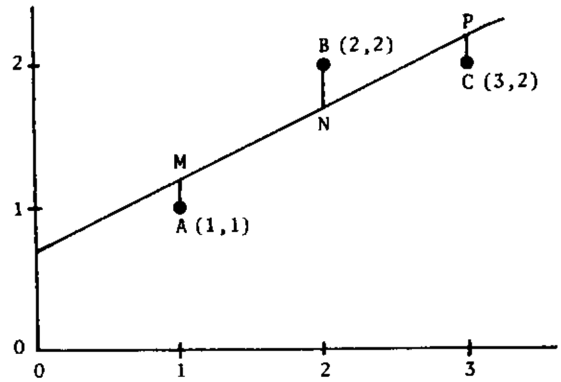


Figure 3. Least squares fit of straight line to three data points. For any other straight line, $|\overline{AM}|^2 + |\overline{BN}|^2 + |\overline{CP}|^2$ will be greater.

points slightly off the curve. Summing the squares takes all the data into account, something like averaging.

According to this criterion the best fit is the one which minimizes the sum of the squares of these vertical distances. It is known as the *least squares fit*. It is possible that it will not pass through any of the data points (see Figure 3).

4.4 How Good is a Good Fit?

After computing the undetermined constants for the "best fit" (whether it be least squares fit or a fit by some other criterion) an experimenter must then decide whether the resulting curve fits well enough. That is, he must see whether the errors are small enough to suit him. How small is "small enough" is a subjective question, but the experimenter cannot reasonably hope for zero error. After all, the mathematical model upon which his curve is based is at best a simplification. Besides there will always be experimental error.

If the errors are "small enough," then we say the curve *agrees with* or *fits* the data.

4.5 Fitting the Graph of f(t) to the Data

In the analysis of digestion we are describing, Blaxter, Graham and Wainman found the least squares fit of Equation (10) for each of the six sets of data depicted in Figure 2. We need not concern ourselves here with the details of computing (k_1, k_2, T), or of deciding if the errors are small enough. The results are shown in Figure 4 for two of the six sets of data. To the naked eye the fits appear to be excellent.

Exercise 9. Assuming that increased stay in the digestive system implies improved digestion, determine from Figure 4 which method of food preparation is more desirable. Why?

---

5. CONCLUSIONS

You may wonder what justification we have for assumptions (A) and (B) in Section 2.2 and the time-delay assumption in Section 4.2. As a matter of fact, there is no convincing way to justify them directly. We do not know whether they are true. But our basic objective was to find a relatively simple and concise way to describe our experimental data, and this we have done, as Figure 4 shows.

In addition, we have certainly provided a starting point for analysis, and some results which strongly suggest that the assumptions may be correct and at least call for further investigation. Blaxter, Graham, and Wainman carry the analysis much further than we have here. Perhaps we should close with a few sentences of theirs (pp. 76-77):

> The interpretation of these constants $[k_1, k_2, T]$ is not rigorous, since there is no proof that k_1 and k_2 apply to events occurring in the specific parts of the tract mentioned; their physiological significance has not been treated by direct experimentation, but...they are certainly extremely suggestive. Attempts were made...to obtain more suitable models, but all soon led to intractable equations. The present equation...has been retained because it fits the data so well and is easily manipulated....

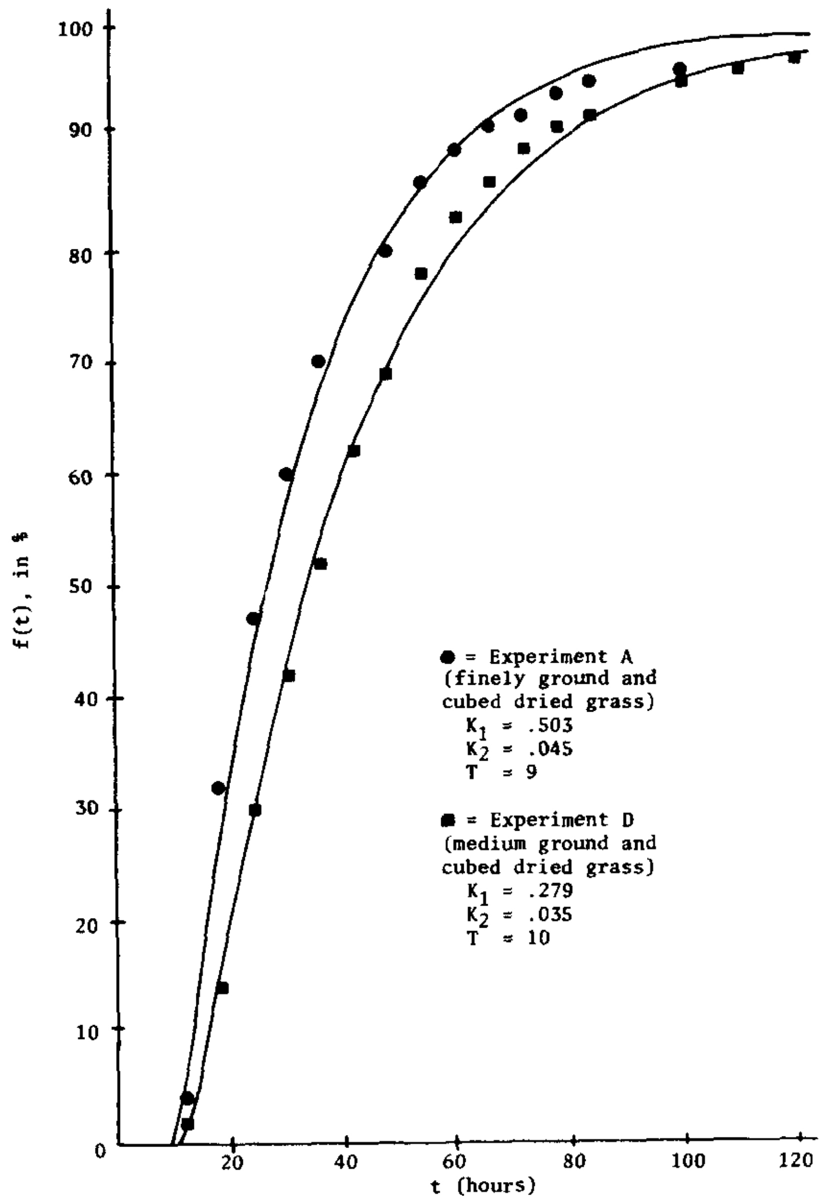


Figure 4. Data from Experiments A and D of Table 1 and Figure 2, with curves fitted from Equation (10). Adapted from Blaxter (1956), p. 76.

The important point, however, is not so much a rigorous physiological interpretation of the constants but that the excretion of stained material can be accurately described by a simple equation with three constants....

6. REFERENCES

1. Batschelet, E. (1976). Introduction to Mathematics for Life Scientists. Springer Verlag, New York.
2. Blaxter, K.L., Graham, N. McC., and Wainman, F.W. (1956). Some Observations on the Digestibility of Food by Sheep and on Related Problems. British Journal of Nutrition, 10: 68-91.
3. Leftwich, A.W. (1967). A Dictionary of Zoology. Constable, London; Van Nostrand, Princeton, NJ.

7. ANSWERS TO EXERCISES

1. $a(t) = k_1 R t e^{-k_2 t}$.

2. (a) $t = \dfrac{\ln k_1 - \ln k_2}{k_1 - k_2}$.

   (b) $\dfrac{k_1 R}{k_2 - k_1}\left[\left(\dfrac{k_1}{k_2}\right)^{-\frac{k_1}{k_1-k_2}} - \left(\dfrac{k_1}{k_2}\right)^{-\frac{k_2}{k_1-k_2}}\right]$

3. $\frac{1}{2}R$.

4. (a) $r'(t) < 0$ for all t.

   (b) $r''(t) > 0$ for all t.

   (c) $\lim\limits_{t\to\infty} r(t) = 0$

5. Letting $t_0 = \dfrac{\ln k_1 - \ln k_2}{k_1 - \ln k_2}$:

   (a) $a'(t) > 0$ for all $t < t_0$
   $a'(t_0) = 0$
   $a'(t) < 0$ for $t > t_0$

   (b) $a''(t) < 0$ for $t < 2t_0$
   $a''(2t_0) = 0$
   $a''(t) > 0$ for $t > 2t_0$

   (c) $\lim\limits_{t\to\infty} a(t) = 0$

6. With t_0 as in Exercise 5:

   (a) $d'(t) > 0$ for all t (must have $k_1 > k_2$)

   (b) $d''(t) > 0$ for $t < t_0$
   $d''(t_0) = 0$
   $d''(t) < 0$ for $t > t_0$

   (c) $\lim\limits_{t\to\infty} d(t) = R$

7. With t_0 as in Exercise 5:

   (a) $f'(t) > 0$ for all $t > T$

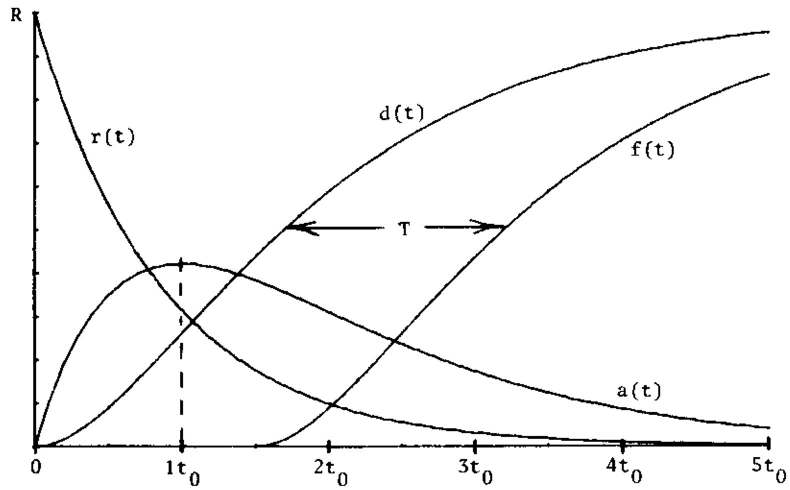
(b) $f''(t) > 0$ for $T < t < T + t_0$

$f''(T + t_0) = 0$

$f''(t) < 0$ for $t > T + t_0$

(c) $\lim_{t\to\infty} f(t) = R$

8.



9. At any time, less of the medium-ground grass has been excreted. Therefore, it tends to stay in the digestive tract longer and, according to the assumption, would be more desirable.