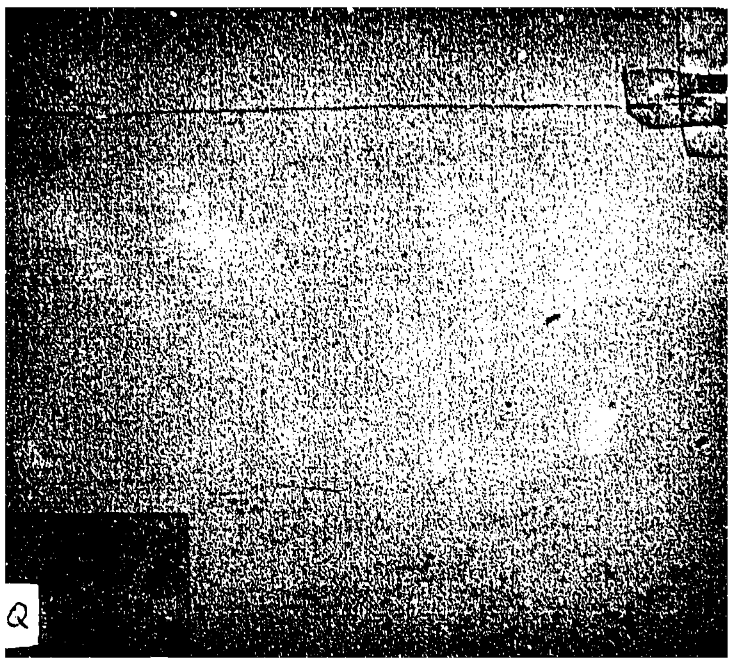
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ABSTRACT

These materials were designed to be used by life science students for instruction in the application of physical theory to ecosystem operation. Most modules contain computer programs which are built around a particular application of a physical process. This module is concerned with the exchange of energy between an organism and its environment in the form of radiation. Classical and modern radiation theory are discussed and the applications of these physical principles to analysis of biological systems are presented. Emphasis in these applications is upon the evolutionary significance of the physical processes. In one type of application, physical theory is used to isolate constant factors in the environment to which all organisms must adjust their evolution. In a second application, physical theory is used to elucidate the constraints governing the evolution of biological systems. It is demonstrated that radiation theory is applicable to a wide range of sense organs, radiation types, wavelengths, and organisms. (Author/CS)

LIGHT AND SOUND: EVOLUTIONARY ASPECTS

by

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INTRODUCTION

All living organisms interact with their environment through a continuous exchange of matter and energy. Conceptually, this can be thought of as a consequence of the "openness" of the system in a thermodynamic sense. For a complete understanding of the biology of an organism, it is essential to determine the ways in which the organism interacts with the biotic and abiotic factors present in the external environment. To most biologists, the exchange of energy between an organism and its environment in the form of radiation is probably the least well understood abiotic factor affecting the organism. As D. Gates has pointed out,[1] this exchange is also the most difficult to measure. However, its importance to the organism cannot be overemphasized.

There are two ways in which the process of radiation exchange is of biological interest. The governing principles of this physical process are different for the two distinct biological applications.

First, there is the dynamical balance of the radiation flow between the organism and its environment, and its effect on the homeostasis of the organism. This dynamical balance is best described by the modern form of radiation theory, which is based on Planck's theory of black body radiation, and which is exemplified in the generally useful results

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[1] [Gates, D. M. "Radiation incident on an organism" 1978, p. 1]

entailed in Wien's law of shift and the Stefan-Boltzmann law. Several simple biological applications of this modern radiation theory are developed in this module. Further applications are presented elsewhere in this series (Gates 1977,1978; Hatheway 1977, Stevenson 1977).

Second, there is the interpretation of the energy received by the organism, as a means of obtaining information about the environment. The selective advantage that results from improved information gathering has led to the evolution of many specialized sense organs. The function of these organs is best described by the classical theory of radiation, particularly as entailed in Rayleigh's criterion and the Doppler effect. The balance of biological examples discussed here are of this second type.

The nature of the physical processes of radiation exchange imposes strong constraints on the evolution of biological systems. This module presents some of the results of classical and modern radiation theory and shows how they elucidate these physical constraints. It is demonstrated that radiation theory is applicable to a wide range of sense organs (eyes, ears, pits); radiation types (electromagnetic, sound), wavelengths (optical, infrared), and organisms.

BLACK BODY RADIATION

In any discussion of radiative energy exchange, it is necessary to begin with an idealization of this process, which is described by the theory of black body radiation. This is rather awkward in the present instance since the biological implications of this abstraction from the real world are not immediately obvious. In fact, some of the most important aspects of biological systems result from their deviations from the idealizations of physics. For example, most organisms are not perfectly "black" in the physical sense of the word; that is, they do not absorb and emit radiation perfectly at all frequencies. The effect of the coloration of organisms will be to vary the degree to which the black body idealization can describe the system. However, it is the nature of science to explain in detail the simple system in the hope that the more complicated systems can be explained by small variations of the simple theory, and the expectation that the major results will be carried over to the more complicated systems. For radiative energy exchange this is precisely the case, and thus there is sufficient justification for presenting a discussion of black body radiation which, though not "simple" in the common sense of the word, is essential for an understanding of the more complicated systems which are the substance of biology.

The theory of black body radiation had a lengthy and fascinating development during the 1800's, culminating in the work of Planck at the turn of the century. Many of the results discussed below were known at various stages during this period of repeated empirical research and hypothesis testing. However, the important results for biological applications can be derived directly from the formula of Planck, which mathematically (though not physically) culminated this field of experimental physics. The physical explanation of Planck's formula awaited the work of Einstein, and ultimately the early founders of Quantum Mechanics.

Planck's problem was to specify the energy distribution of the electromagnetic radiation within a cavity, the walls of which are at thermal equilibrium at the temperature T. That is, the problem is to find the energy density $E(\nu)$ ($J\ s\ m^{-3}$) of the radiation within the cavity between the frequencies ν and $\nu + d\nu$. The shape of the curve $E(\nu)$ vs. ν had been determined experimentally at various temperatures [Fig. 1] . Planck found a solution to this problem in the form:

$$E(\nu) = \frac{8\pi h\ \nu^3}{c^3} \left[e^{h\nu/kT} - 1\right]^{-1}$$

where ν is the frequency of the radiation, T is the absolute temperature of the walls of the cavity, and h, k and c are physical constants [see Appendix 1]. This energy distribution is called the black body energy distribution because it is the same as the energy distribution of radiation emitted by a perfectly black object which is at absolute temperature T. For measurement purposes, it is more useful to express this energy density in terms of the wavelength λ.

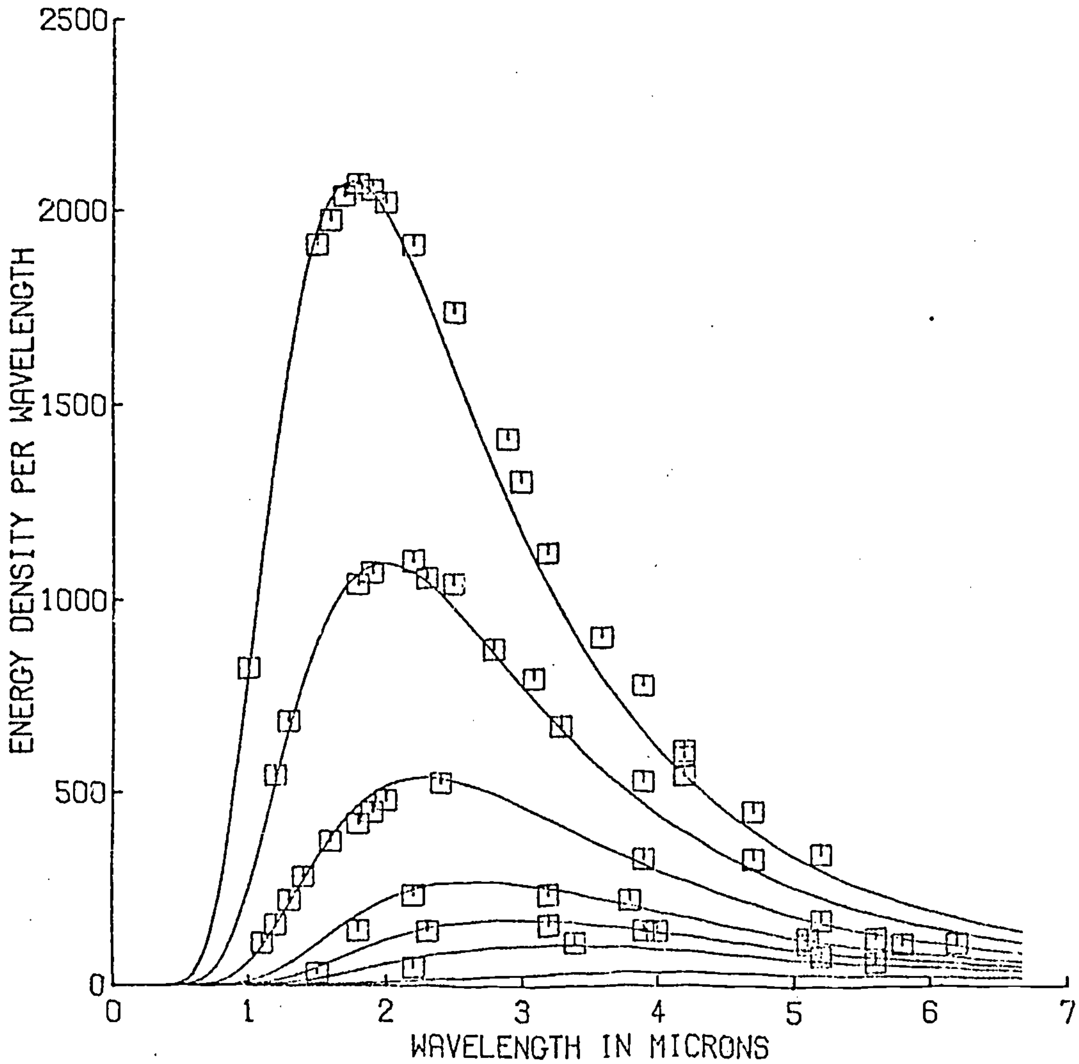
Problem 1

Show that the energy density per unit wavelength is given by:

$$E(\lambda) = \frac{8\pi hc}{\lambda^5} [e^{hc/\lambda kT} - 1]^{-1}$$

Hint: $\lambda = c/\nu$

FIGURE 1- BLACKBODY RADIATION PLANCK'S LAW VS. OBSERVED DATA FROM LUMMER AND PRINGSHEIM (1901)



CURVES- PLANCK'S LAW FOR T= 1646, 1449, 1259, 1095, 998, 904, 723

Wein's Law of Shift

It can be shown that the $E(\lambda)$ distribution can be described by the wavelength λ_m at which the distribution reaches its maximum. Qualitatively increasing the temperature T shifts the maximum of the $E(\lambda)[E(\nu)]$ curve to a smaller λ (higher ν).

Example 1

The wavelength at which the energy density is a maximum at a given temperature T can be found as follows:

From problem 1:

$$E(\lambda) = \frac{8\pi hc}{\lambda^5}\left[e^{hc/\lambda kT} - 1\right]^{-1}.$$

Make the substitution $u = hc/\lambda kT$:

$$E(\lambda) = \frac{8\pi k^5T^5}{c^4h^4}\left[\frac{u^5}{e^u - 1}\right].$$

From calculus, the maximum can be found by solving:

$$\frac{dE}{du} = 0, \quad \text{which gives}$$

$$\frac{dE}{du} = \frac{8\pi k^5T^5}{c^4h^4}\left[(5u^4)(e^u-1)^{-1} - e^u(u^5)(e^u-1)^{-2}\right] = 0 \quad \text{or}$$

$$\left[(5u^4(e^u-1) - u^5e^u)(e^u-1)\right]^{-2} = 0 \quad \text{which implies}$$

$$5u^4e^u - 5u^4 - u^5e^u = 0 \quad \text{or finally:}$$

$$e^{-u} + 1/5u - 1 = 0.$$

This transcendental equation can be solved by numerical techniques (see Appendix 2) to give:

$$u = 4.9651\ldots\ldots\ldots$$

Thus

$$\lambda_m T = \frac{hc}{uk} = 2.8978 \times 10^{-3} \mathrm{m\ K} = b.$$

b is called the Wien constant and the equation

$$\lambda_m T = b$$

is called Wien's law of shift (1896 Wilhelm Wien). Therefore, the maximum of the black body curve $E(\lambda)$ at temperatures $T_1, T_2, T_3, \ldots$ falls at $\lambda_1, \lambda_2, \lambda_3, \ldots$ so that

$$\lambda_1 T_1 = \lambda_2 T_2 = \lambda_3 T_3 = b$$

[see Fig. 2].

The Wein law of shift is a very powerful result because it embodies a single relation between wavelength and absolute temperature. This is exemplified in the following problem.

Problem 2

Assuming the following objects radiate as black bodies, what is the λ_m for:

a) the sun at $T_s = 5700$ K

b) a mammal with a surface temperature $T = 37°C$

c) a lizard with a surface temperature $T = 10°C$

d) the clear night sky, radiation temperature $T = -33°C$

Answers:

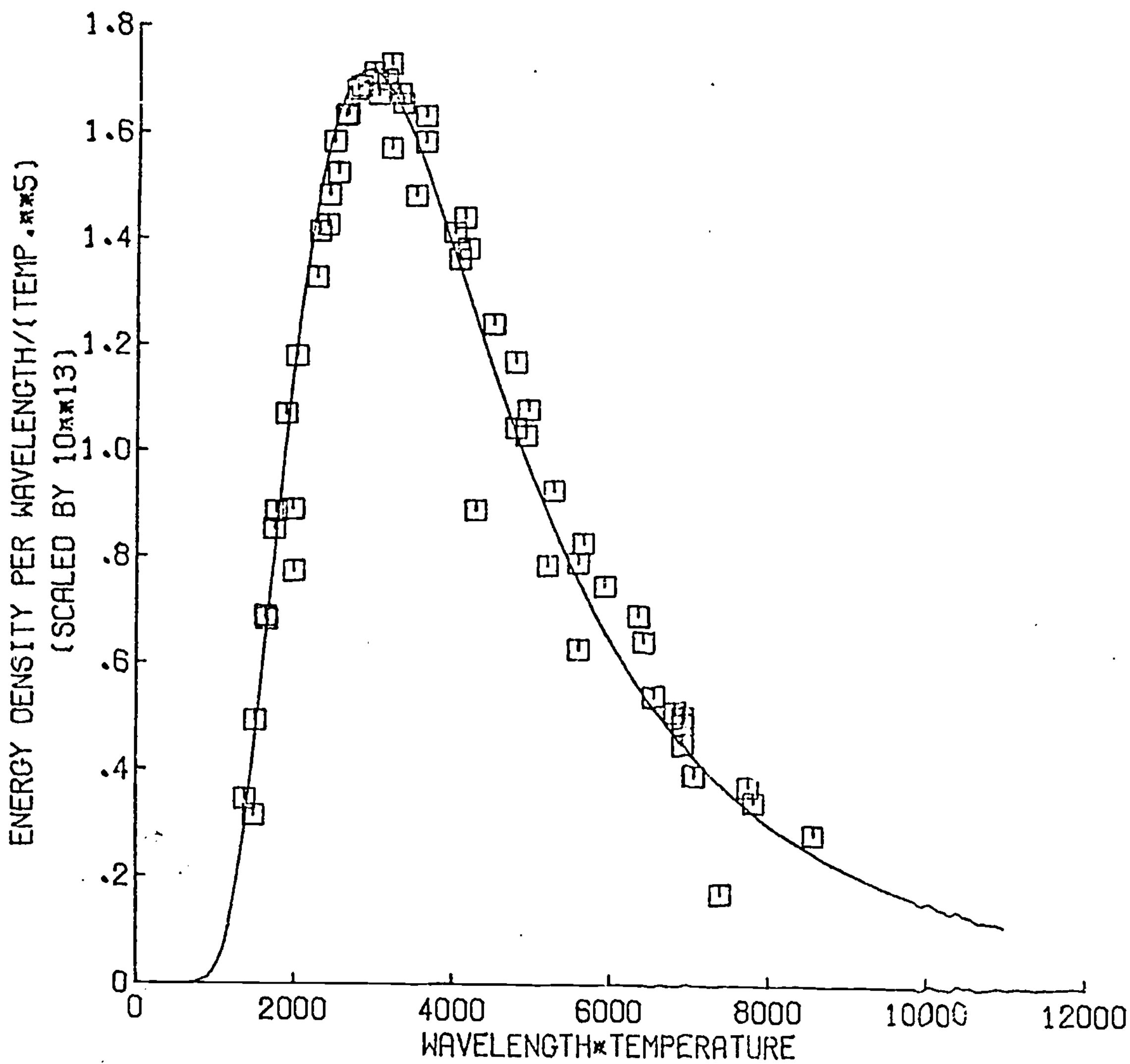
a) 5.08×10^{-7}m = 5080 Å (yellow)

b) 9.66×10^{-4}m (infrared)

c) 1.024×10^{-3}m (infrared)

d) 1.21×10^{-3}m (infrared)

FIGURE 2- WIEN:S LAW- OBSERVED VS. PREDICTED
SAME DATA AS IN FIG. 1.



Stefan-Boltzmann Law

If E is the total energy density in all frequencies (J m^{-3}):

$$E = \int_0^\infty E(\nu)d\nu = \frac{8\pi h}{c^3}\int_0^\infty \frac{\nu^3 d\nu}{e^{h\nu/kT} - 1} \quad . \qquad (1)$$

Making a change of variable,

$$x = h\nu/kT \text{ which implies } d\nu = \frac{kT}{h}dx.$$

Equation (1) becomes

$$E = \frac{8\pi h}{c^3}\left(\frac{kT}{h}\right)^4 \int_0^\infty \frac{x^3 dx}{e^x - 1} \qquad (2).$$

The value of the integral in Equation (2)

$$I = \int_0^\infty \frac{x^3 dx}{e^x - 1} \qquad (3)$$

can be obtained by numerical integration. This is a technique for approximating a definite integral by a finite sum. The value of the integral in Equation (3) is found in Appendix 2 to be:

$$I = 6.4983.$$

Equation (2) can be re-expressed as

$$E = \left[\frac{8\pi h}{c^3}\left(\frac{k}{h}\right)^4 I\right] T^4 = aT^4 \qquad (4)$$

where the constant a is equal to the value of the constants in the square brackets in Equation (4). The value of a is found to be

$$a = \frac{8\pi h}{c^3}\frac{k^4}{h^4}(6.4983) = 7.5643 \times 10^{-10} \text{ J m}^{-3} \text{ K}^{-4}.$$

The energy radiated by a black body per unit area per unit time, that is, the radiation emittance E_n, can be shown to be

$$E_n = \sigma T^4 \tag{5}$$

where $E_n \equiv$ radiation emittance and

$\sigma = (\frac{1}{4})ca = 5.6693 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$.

Equation (5) is called the Stefan-Boltzmann law and the constant σ is called the Stefan-Boltzmann constant. Although Equation (5) is quantitatively precise, the functional relationship of the variables is more important than the exact numerical value of the constants. Of particular interest is that the radiation emittance is proportional to the fourth power of the absolute temperature.

The equation is of direct biological interest when it is realized that the Stefan-Boltzmann law governs the radiative energy exchange between an organism and its environment. Although this exchange of energy is usually not considered when calculating the energy budget of an organism, it can in some circumstances be a major factor affecting the heat balance of an organism. The following example and problem constitute a brief introduction to the application of this physical law to biology. For a more detailed exploration of this relationship, see Gates (1978) and Hatheway (1977).

Example 2

A bat with a surface temperature of 37°C is living in a cave which has walls at a temperature of 12°C. What is the radiation emittance of the bat? If the bat has a total surface area of 100 cm^2, what is its rate of heat loss by this process of radiative exchange?

Solution: Define

$T_o \equiv$ the bat's surface temperature (in K)

$T_a \equiv$ the ambient temperature (i.e., the temperature of the cave) (in K).

Clearly the bat is emitting radiant energy at the rate:

$$E_o = \sigma T_o^4$$

and receiving radiant energy (from the walls) at the rate:

$$E_a = \sigma T_a^4.$$

So the overall energy exchange by this process is given by:

$$E = \sigma(T_o^4 - T_a^4)$$

with the convention that E is positive when the overall radiation balance is such that the bat is emitting more than it absorbs; i.e., it is losing energy to the environment at the rate E.

For this example:

$$T_o = (273 + 37)\ K = 310\ K$$

$$T_a = (273 + 12)\ K = 285\ K$$

which gives an energy emittance of:

$$E = 5.67 \times 10^{-8} (W\ m^{-2}\ K^{-4})\ [(300\ K)^4 - (285\ K)^4]$$

$$= 5.67 \times 10^{-8} [9.235 \times 10^9 - 6.598 \times 10^9]\ W\ m^{-2}$$

$$= 5.67\ [92.35 - 65.98]\ W\ m^{-2}$$

$$= 149.5\ W\ m^{-2}$$

The bat's total heat loss rate H, by this process is

$$H = E(SA)$$

where SA = surface area, so

$$H = 149.5\ W\ m^{-2}\ (100\ cm^2)$$

$$= 1.495\ W.$$

Although in this example the heat loss rate was relatively small, when there are larger differences between the organism's temperature and the (radiation) temperature of the environment, the heat loss rate can be quite high. This situation pertains in the following problem.

Problem 3

a) The horns of a reindeer are at approximately internal body temperature, though the rest of the deer's body is well insulated. If these horns are at a temperature (T_o) of 32°C, and they have a surface area of 1000 cm^2, what is the heat loss rate if the environment is at a (radiation) temperature (T_a) of -10°C? Convert your answer to calories/minute.

[See Gates 1968 for some actual organismal temperature measurements.]

Answer: $H \approx 22$ W.

b) A bald mountaineer is outside on a clear night. Although he is heavily bundled in his down parka, he has forgotten his hat. If his bald pate has a surface area of 75 cm^2 and is at a temperature of 32°C, what is his heat loss rate to the night sky which is at a (radiation) temperature of -45°C? [Is this why they say, "If your feet are cold, put on your hat."?] Convert to calories/minute.

Answer: $H \approx 25.3$ W = 362 cal/min.

The solar constant

A physical parameter which imposes a significant constraint upon the evolution of terrestrial organisms is the amount of energy generated by the sun which is intercepted at the earth's surface. Almost all of the energy which drives the biological processes on the earth comes directly or indirectly from the sun. Thus the amount of the sun's energy that the earth receives is of interest for at least two reasons: (1) This is the upper limit to the amount of energy that could be absorbed by a surface and turned into heat. (2) This is the upper limit to the amount of energy that could be converted by a photosynthetic unit into chemical energy. Since the actual amount of sunlight available at the earth's surface is dependent upon absorption by the atmosphere, and thus on such variables as latitude, the sun's altitude in the sky (see Gates 1978, section on Direct Solar Radiation), or cloudiness, the measure of the sun's energy available at the earth is determined instead for a unit area just outside the earth's atmosphere. This measure of the sun's energy (actually the rate of the available energy, i.e., power) is called the <u>solar constant</u>.

The solar constant can be calculated theoretically from the Stefan-Boltzmann law and conservation of energy. Assuming the sun to be a black body with a surface temperature T_s, by the Stefan-Boltzmann law, its radiation emittance (energy radiated per unit area per unit time) is given by:

$$E_s = \sigma T_s^4. \tag{5}$$

Thus the total power emitted by the sun can be found by integrating E_s over the sun's surface. Since T_s is (assumed to be) constant, this is equivalent to multiplying the constant E_s by the surface area of a sphere with the sun's radius (r_s). The total power is given by:

$$E = 4\pi r_s^2 E_s. \tag{6}$$

By conservation of energy, if no energy is lost in the intervening space, all of the radiation emitted radially out from the sun will be intercepted by an (imaginary) sphere centered on the sun with a radius equal to the mean distance from the sun to the earth (r_E). The power flow per unit area (E_E) across this (imaginary) sphere will be equal to the total power available (E), divided by the surface area of the sphere ($4\pi r_E^2$). That is,

$$E_E = E/4\pi r_E^2. \tag{7}$$

Substituting Equation (6) in Equation (7) gives

$$E_E = \frac{4\pi r_s^2 E_s}{4\pi r_E^2} = \frac{r_s^2}{r_E^2} E_s \quad . \tag{8}$$

The quantity E_E which is the power available (per unit area per unit time) on a surface at the earth's distance from the sun, is the parameter of interest, the solar constant.

Inserting Equation (5) into Equation (8) gives immediately:

$$E_E = \left(\frac{r_s^2}{r_E^2}\right) \sigma T_s^4. \tag{9}$$

Problem 4

Use Equation (9) and the following physical parameters to calculate the solar constant:

$T_s = 5700$ K

$r_s = 7.1 \times 10^8$ m

$r_E = 1.49 \times 10^{11}$ m

$\sigma = 5.6693 \times 10^{-8}$ W m^{-2} K^{-4}

Convert your answer to cal cm^{-2} min^{-1}.

Answer: $E_E = 1.36 \times 10^3$ W m^{-2} s^{-1} $\approx$ 1.95 cal cm^{-2} min^{-1}.

III. Resolution

For most problems of biological interest (e.g. the shape of the lens of the eye), only the particulate nature of light, especially its rectilinear propagation, is important. This can be thought of as a result of the large size of the elements of biological interest compared to the wavelength of light. For example, for the sun: $\lambda_m \approx 5 \times 10^{-7}$m [problem 2a], which is much smaller than the physical dimension of any organism, or even any organ in any organism. Only in certain specialized biological research, for example the investigation of cell ultrastructure, does the wavelength of light become a limiting factor. As the dimensions of the cellular constituents approximate that of light, instruments capable of observing at shorter wavelengths (e.g. electron microscopes) are required.

There is at least one other area of biology where the physical dimensions of the objects of interest are small enough that the wave nature of light becomes an important consideration: the resolution of incoming radiation by sense organs.

The term resolution is used here to denote the ability to distinguish two objects. That is, how close together must two objects be before they appear as a single object to the organism? Clearly, this depends to some extent on the organism in question; eagles resolve better than do moles. Also, the limit of resolution will be affected by the experience of the observer. Nevertheless, it is useful to have some rough comparison of the resolving ability of various systems, and for this purpose Rayleigh's criterion is most often employed.

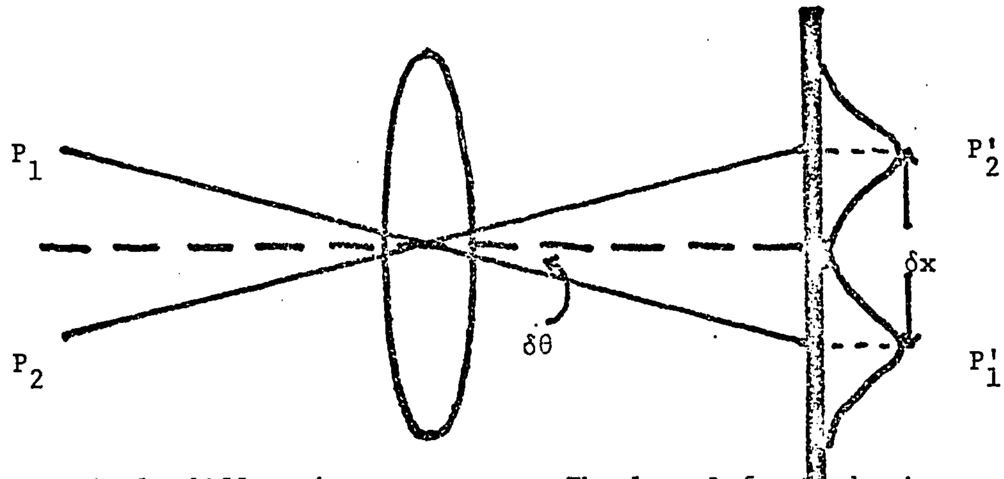
Rayleigh's criterion is derived from the theory of Fresnel diffraction by a circular opening (for a derivation and detailed discussion, see Elmore & Heald 1969). Qualitatively, this criterion is seen to be a measure of the relative overlap of the diffraction patterns of the images of objects on the focal plane of the observer. More specifically, it is a measure of the displacement of the central maxima of these diffraction patterns. Two images are said to be just resolved when the central maximum of one diffraction pattern falls on the first minimum of the other (see Fig. 3).

From Figure 3, it can be seen that the limit of resolution is some distance δx between the two images on the focal plane, or alternatively some angle $\delta\theta$ between the central axis of the lens and the ray connecting the center point of the lens to the centers of the principal maxima on the focal plane [p_1',p_2' of Fig. 3]. Therefore, in comparing the resolving power of different instruments the reciprocal of these quantities should be used (i.e., $1/\delta x$ or $1/\delta\theta$), so that the "more powerful" instrument is able to distinguish objects which are unresolved by the "less powerful" instrument. For a distant object, the objective (lens) is the aperture which creates the circular diffraction. The mathematical details of Fresnel diffraction lead to the result that the position of the first minimum relative to the principal maximum will be:

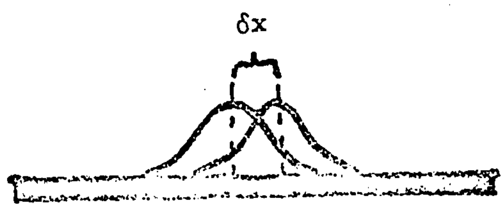
$$\sin \alpha = 0.61\ \lambda/r \qquad (11)$$

where

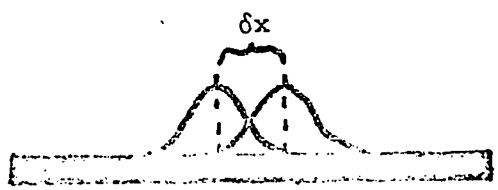
Figure 3: The Rayleigh criterion: Fresnel diffraction by circular aperture.



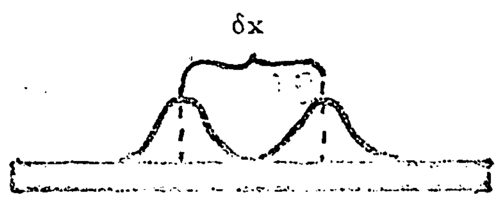
a) A simple diffraction apparatus. The lens L forms the images of the point sources P_1 and P_2 on the focal plane F. These images are not points but disks centered at P'_1 and P'_2 whose intensity is greatest at the center as indicated by the "humps" behind the focal plane. [From Sears and Zemansky p. 619



b) Diffraction patterns almost coincident: unresolved.



c) Diffraction patterns with the first minimum of the image of object 2 falling on the principal maximum of the image of object 1: just resolved. (This is the Rayleigh limit.)



d) Fully resolved.

λ = the wavelength of radiation which forms the image,

r = the radius of the objective,

α = the angle between the images of the objects.

The limit to resolution given by Eq. (12) is known as Rayleigh's criterion. Using the familiar (Taylor) expansion of the sine function one finds that:

$$\sin \alpha = \alpha - \alpha^3 + \alpha^5 - \alpha^7 + \ldots$$

or $\quad \sin \alpha = \alpha + 0(\alpha^3)$.

Here $0(\alpha^3)$ means terms of order (size) strictly less than α^3. If α is small, then α^3 is very small and one can make the small angle approximation

$$\sin \alpha \approx \alpha$$

which when substituted into Eq. (11) yields:

$$\alpha = 0.61\, \lambda / r \, . \qquad (12)$$

Rayleigh's criterion in the simple form of Eq. (12) is a powerful tool in an analysis by the biologist of the evolution of sense organs. In particular, such questions as the scaling of eye size with organismal size (e.g., why are a whale's eyes the same size as those of a cow?), or the cellular organization of the organs themselves (e.g. the distribution of cones on the retina) have relatively simple answers when analyzed in this way. The ramifications of this analysis are explored in the following examples and problems.

<u>Example 4</u>

From the Rayleigh criterion, the results of problem 2a, and the fact that in bright daylight the diameter of the human pupil is ≈ 2.0 mm, determine the resolution of the human eye in minutes of arc. What does this resolution limit correspond to at 10 m?

Solution: $\lambda_m = 5.08 \times 10^{-7}$m (from prob. 2a)

$r = 1.0$ mm $= 1.0 \times 10^{-3}$m.

Putting these parameters into the formula for the Rayleigh criterion, Eq. (12), we get:

$$\alpha = .61\ \lambda/r$$

$$= 0.61(5.08 \times 10^{-7}\text{m})/(1.0 \times 10^{-3}\text{m})$$

$$= 3.1 \times 10^{-3} \text{ radians.}$$

Since 2π radians = 360° = 2.16×10^4 min, we know that

$$1 \text{ radian} \approx 3.43 \times 10^3 \text{ min.}$$

So

$$\alpha = (3.1 \times 10^3 \text{ min/rad})(3.1 \times 10^{-3} \text{ rad})$$

$$\approx 1 \text{ min of arc.}$$

At 10 m this angle will correspond to an object separation of:

$$\alpha = S_o/d$$

where S_o = separation

d = distance

or $S_o = \alpha d = (3.17 \times 10^{-4})(10\text{m}) = 3.117 \times 10^{-3}$m

$= 3.17$ mm.

Thus, in daylight the human eye can just barely resolve two objects which are 3.17 mm apart from one another and 10 m distant.

It should be noted at this point that the Rayleigh criterion is a theoretical limit which is rarely approached in practice. For instance, if one used this formula to calculate the separation resolvable by the human eye at 20 ft., it would be smaller than the actual minimum separation resolvable by a person with "normal" (20:20) eyesight.

Problem 5

The cones of the human eye happen to be maximally sensitive to the wavelength λ_m which corresponds to the maximum of the sun's energy density spectrum. Using Rayleigh's criterion and the fact that the retina is $\simeq$ 17 mm behind the first nodal point (which acts as the circular aperture in this case), compute the maximum resolution on the surface of the retina.

Answer: $\delta x = 5.4 \times 10^{-6}$m. (13)

Anatomists have determined that the diameter of a retinal cone cell (which mediates color vision) is about 3.0×10^{-6}m. The separation between densely packed cone cells is smaller than the limit in Eq. (13). Thus thinner cones will not produce higher visual acuity. The resolution is constrained by the physical parameters of the optical system.

Since the eyes of all vertebrates are constructed from the same design, the same physical dimensions that determine the resolution of the human eye will determine resolution throughout the subphylum. It is the absolute, not relative, size of the physical components of the optical system which constrain resolution. If the diameters of cone cells are at present at the minimum which is biologically feasible, then a slight increase in the other dimensions of the human eye will give greater resolving power, but beyond a point ($\delta x = 3.0 \times 10^{-6}$m), there is no payoff in visual acuity for larger eyes.

The eyes of birds of prey show structural alterations which are an evolutionary response to the need for greater resolving power. The retinal cone cells become rod-like, which decreases their diameter, increases their density on the retina and decreases their ability to discriminate color. Furthermore, the retinae from these birds have several pits or foveae. Although the density of light sensitive cells is the same in the foveae as on the rest of the retina, the image is formed on a concave rather than flat surface. Thus the "effective" cone density in the foveae is higher than for the rest of the retina, and so is the resolving power. The combination of these two changes results in increased visual acuity for these avian eyes.

Rayleigh's criterion is also useful in elucidating the constraints on the design of a quite different sort of eye, the compound eye found in insects and certain crustacea. Each eye is composed of many (up to 3×10^4) simple eyes, called ommatidia (See e.g. Björn 1976. p. 92). The shape of the compound eye is roughly that of a half-sphere of radius R, with the lenses of the ommatidia comprising its surface. An estimate of the size of the openings of the ommatidia is calculated in the following problem.

Problem 6

A simple model of an ommatidium is that of a cone with its apex at the center of the half-sphere which forms the eye, and its opening at the surface of the eye. Assume that the angle of the cone is equal to the limiting angle of the Rayleigh formula. Show that the calculated limiting size of the opening to the ommatidia is given as:

$$d = (1.22R\lambda)^{1/2}$$

If λ = 400 nm, which is the center of the spectrum to which a bee is sensitive, and R is about 1 mm, what is the optimal size of the ommatidial opening?

Answer:

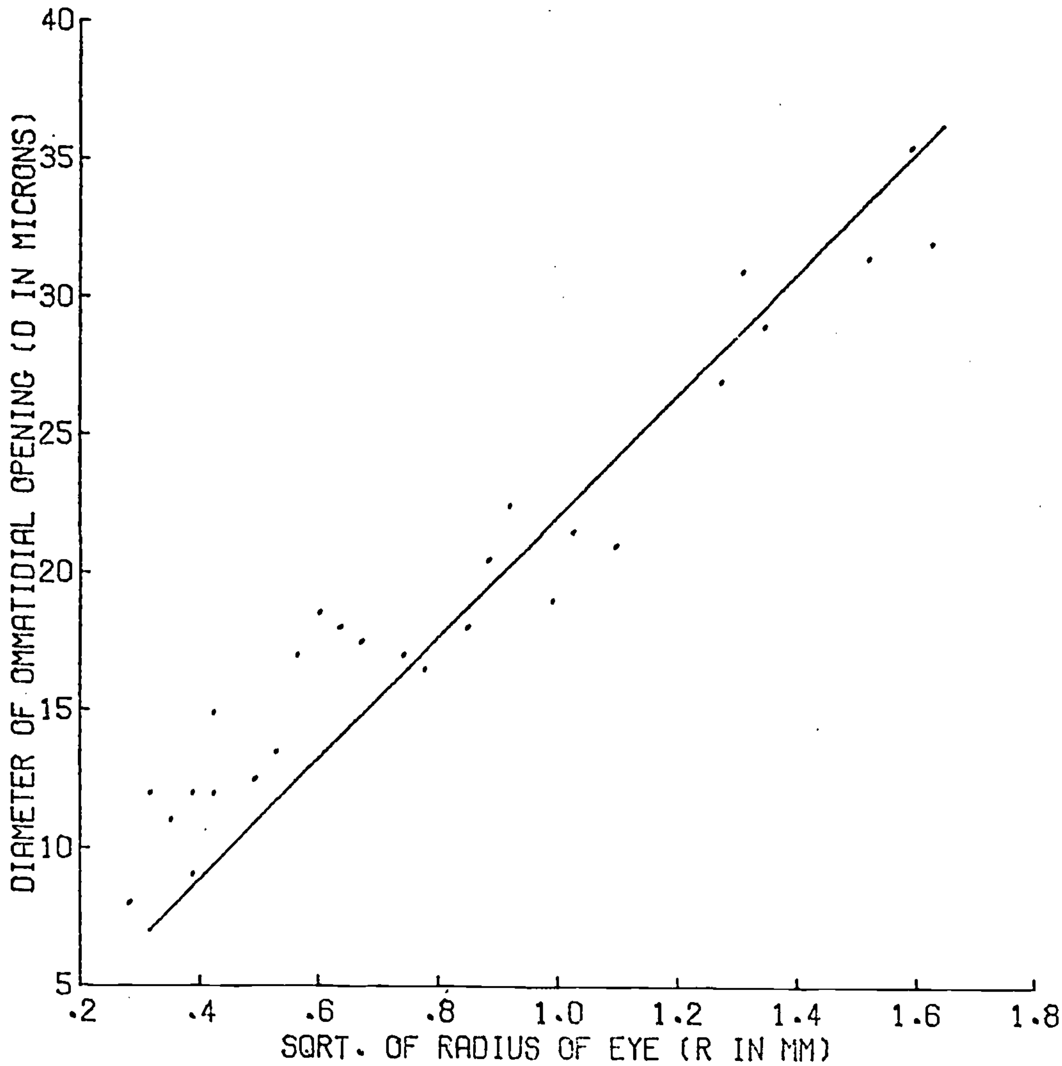
$$d = 2.2 \times 10^{-5} \text{ m} = 22\ \mu.$$

The actual mean measured opening for a bee is 20.9 μ (Barlow 1952, p. 671). A diagram comparing the observed size of the ommatidia to the value predicted by theory is presented in Fig. 4.

Rayleigh's criterion for the limit of resolution of an optical instrument can be extended to interferometers as well. Basically, an interferometer consists of two detectors with the ability to detect phase information separated by a distance D. When the phase information from the two detectors is compared, the resolution of the total system is the same as that of a single detector whose diameter is equal to D. Although a rigorous argument demonstrating this result would not be appropriate here (it is essentially the same as the derivation of Rayleigh's criterion), a qualitative argument may be useful. Basically, the diffraction patterns illustrated in Fig. 3 are the result of the interference between light waves of different phases, caused by passage of the light through the aperture. The eye sees the interference caused by phase differences as variations in intensity, as illustrated in Fig. 3 b, c, d. In an interferometer the signals of the two detectors are compared to reveal phase differences and so the identical resolution criterion applies.

Most vertebrates are able to detect phase differences between ears, so that the interferometer is the correct model for calculating resolution. A consideration of Rayleigh's criterion shows that if all other parameters remain constant, the greater the separation of the detectors, the greater

FIGURE 4. INSECT EYE. OMMATIDIAL DIAMETER VS. SQRT. EYE RADIUS
POINTS. 27 OBSERVATIONS ON HYMENOPTERA (BARLOW 1952)



LINE. PREDICTED BY RAYLEIGH CITERION (SEE PROBLEM 6) the resolving power of the system. Many organisms have optimized their ability to locate sound sources by maintaining a maximal separation between the ears. Another biological application of interferometers is illustrated in the following problem.

Problem 7

Using the Rayleigh criterion and the solution to Prob. 2b, determine the resolution of the infrared sensing system of a pit viper. Using reasonable physical parameters (e.g. body size of prey, how close the snake must be to strike, how accurate the strike has to be), determine the minimum separation of the pits. Does this agree with your intuition and/or experience?

Answer: d = separation of pits $\approx$ 6 cm.

IV. The Doppler Effect

The discussion up to this point has implicitly assumed that the source and detector of radiation are stationary relative to one another. When the source and detector are in relative motion, an added complication, the Doppler effect, is introduced. This phenomenon has been observed for all types of radiation, though the theory is simplest for the acoustic situation. Since acoustic waves are longitudinal (compression) rather than transverse as are electromagnetic waves, the mathematical form of the effect is slightly different. Additionally, the acoustic Doppler effect has significant evolutionary implications.

Empirically, the Doppler effect is manifested in the difference between the pitch (frequency) of the sound heard by a listener in motion relative to a sound source and the pitch heard when the listener and source are relatively stationary. A familiar example is the sudden drop in pitch one hears from an automobile horn as one meets and passes a car going in the opposite direction. Alternatively, one might think of the changing pitch heard by a listener standing beside a track as a train whistle approaches, passes, and recedes.

The derivation presented below is for the Doppler effect as it applies to the special case when the motion of the source and listener lies along the line joining the two. The biological example considered later is of precisely this type.

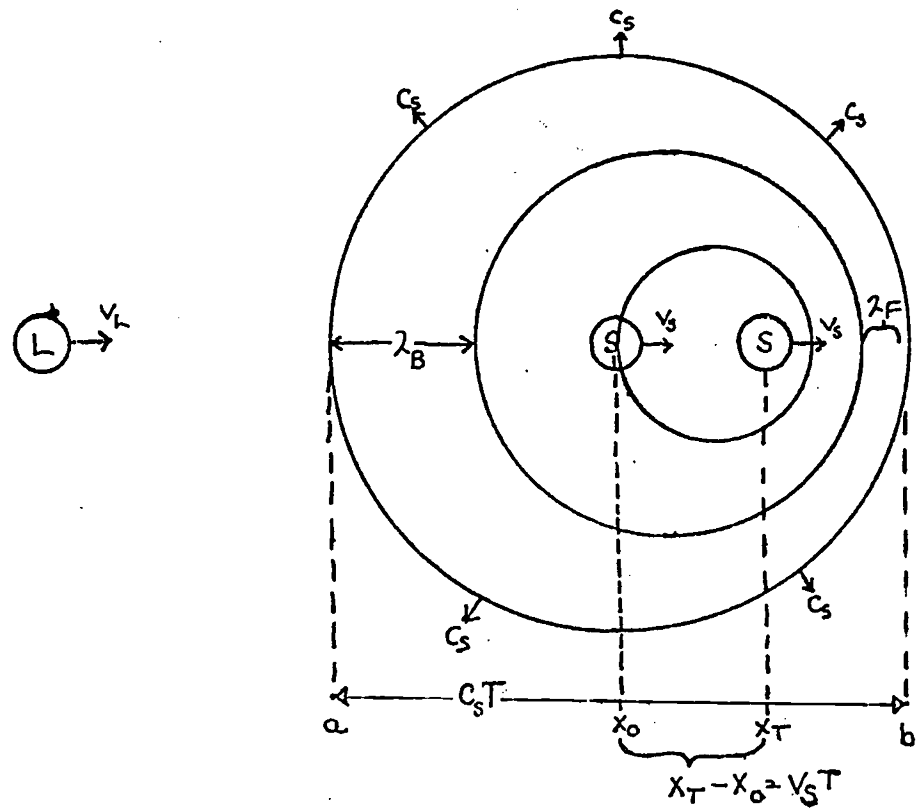
Let V_L and V_S denote the velocities of the listener and source respectively. The positive direction for the velocities is taken to be from the position of the observer to the position of the source.

An illustration of the situation when the listener L and the source S are moving away from each other is presented in Fig. 5. At time $t = o$, the source is at point X_T. The outermost circle is the representation of the position of the wave front at time $t = T$, caused by a disturbance at the source at time $t = 0$. The speed of propagation C_s of a wave in a nondispersive medium such as air is dependent only upon the characteristics of the supporting medium and is independent of the motion of the source relative to the medium. Thus the outermost circle in Fig. 5 represents a sphere in 3 dimensions with center at x_o and radius C_sT.

The source has moved a distance V_sT in the time T so that

$$x_o - x_T = V_sT$$

Figure 5: The Doppler Effect



The source S, moving with velocity V_S, is emitting sound at a constant frequency, f_S. The wave fronts of this sound, which travel radially outward at velocity C_S, are compressed together (wavelength equals λ_F) in front of the source and spread out (wavelength equals λ_B) behind the source. By the time the wavefront emitted by the source at x_0 at time $t = 0$ has reached a radius of C_ST, the source has moved to a position x_T. The listner L moving with velocity V_L will hear the sound at a different frequency than as actually emitted by the source because it encounters wave fronts which are λ_B apart. An exact derivation is given in the text. [Adapted from Sears and Zemansky p. 327.]

and the following equalities are true:

$$a - x_T = (C_s + V_s)T$$

$$x_T - b = (C_s - V_s)T$$

where a and b are respectively the positions at the rear and front of the outermost wave surface.

In the time interval between t = o and t = T, the source has emitted a certain number of waves, f_sT, where f_s is the frequency of the sound emitted at the source. The waves are spread out into the distance $(x_T - b)$ in front of the source.

In front of the source the wavelength λ_f is given by

$$\lambda_f = \frac{x_T - b}{f_sT} = \frac{(C_s - V_s)T}{f_sT} = (C_s - V_s)/f_s.$$

Similarly behind the source the wavelength λ_B is

$$\lambda_B = \frac{a - x_T}{f_sT} = \frac{(C_s + V_s)T}{f_sT} = (C_s + V_s)/f_s.$$

The waves approaching the listener have a relative speed of $C_s + V_L$, so the detected frequency is

$$f_L = (C_s + V_L)/\lambda_B = \frac{C_s + V_L}{(C_s + V_s)/f_s}$$

or

$$f_L = \frac{C_s + V_L}{C_s + V_s} f_s. \tag{14}$$

When the source and listener are moving toward each other a frequency

$$f_L = \frac{C_s + V_L}{\lambda_f} = \frac{C_s + V_L}{(C_s - V_s)/f_s}$$

or

$$f_L = \frac{C_s + V_s}{C_s - V_s} f_s \qquad . \qquad (14a)$$

is detected.

In order to help remember the direction convention established in this derivation, it is useful to notice that the frequency heard by the listener will be less than that emitted by the source if they are moving away from each other, and will be greater than that emitted by the source if they are moving toward each other.

Example 5

The velocity of sound in still dry air is $C_s = 350\ \mathrm{m\,s^{-1}}$. For a source emitting sound of frequency $f_s = 700$ Hz the wavelength of the sound emitted is

$$\lambda = C_s/\lambda_s = 0.5\ \mathrm{m}.$$

a) What are the wavelengths of the sound in front of and behind this source moving at $V_s = 50\ \mathrm{m\,s^{-1}}$?

b) If a listener is at rest and this source is moving away at $V_s = 50\ \mathrm{m\,s^{-1}}$, what is the frequency of the sound heard?

Solution:

a) $\lambda_F = (C_s - V_s)/f_s = 0.429$ m

$\lambda_B = (C_s + V_s)/f_s = 0.571$ m

b) $f_L = \dfrac{C_s}{C_s + V_s} = 612$ Hz.

Now that a quantitative formulation of the Doppler effect has been derived, it can be applied in the explanation of echolocation in bats, a sensory system which has only begun to be understood in the past several decades.

The bats, members of the order Chiroptera within the class Mammalia, have developed a system of echolocation which has been of immense evolutionary significance. It has enabled them to exploit a resource for which there are very few competitors, small night-flying insects (see, e.g., Fenton 1974). The physical processes important in echolocation have both enhanced and constrained the evolution of the Chiroptera. Here it will suffice to show a few examples of the effect of these physical processes upon bat evolution and natural history. For a detailed and personable account of the actual experimentation that led to the elucidation of the physical principles employed in echolocation, see Griffen's Listening in the Dark (Griffen 1958).

Almost all bats appear to be able to navigate in total darkness a closely spaced grid of wires, where the spacings of the wires are commensurate with the dimensions of the wingspread of the bats. Furthermore, insectivorous bats can pursue and capture flying insects on the wing in total darkness.

The ability to carry out these activities is significant in two respects. First, unlike the birds which are able to perform similar activities only in the presence of light, bats cannot be dependent upon a highly developed sense of sight for navigation. Second, no other animal can depend upon catching flying insects in the dark and so there are few competitors for this food resource. Prior to the evolution of bats, this resource had not been exploited.

The experiments of Griffen demonstrate that bats share another ability that sets them apart from most other animals. This is the ability to produce and detect sound of frequencies between 20-100 kHz. It is this attribute which is fundamental to the system of echolocation, as in the next example.

Example 6

A flying bat emits a pulse of sound. What is the minimum frequency and maximum length of a single frequency pulse, if the bat wants to use the echo of the pulse to avoid an obstacle 1 meter ahead?

Solution: One first solves for the maximum pulse length. Clearly the chief consideration is that the bat must not be producing the pulse when the echo returns. Otherwise the fainter echo might be masked by the bat's own cry. The time of the echo's return t is dependent only on the speed of sound C_s and the distance of the object d. Specifically:

$$t = d/C_s$$

which works out to be:

$$t = 2\ \text{m}/350\ \text{m s}^{-1} = 5.71 \times 10^{-3}\ \text{s} = 5.71\ \text{ms}.$$

Shorter pulses will allow even closer objects to be avoided, although the pulse length must have a lower limit of several wavelengths in order to avoid problems in interpretation. If a reasonable number of waves in the pulse is 100, the predicted minimum frequency would be:

$$f = 100/t = 100/4 \times 10^3\ s^{-1} = 25\ kHz.$$

In actual field measurements Griffen (op cit. p. 191) has observed pulse lengths from 1-15 ms , and pulse frequencies between 30-75 kHz with about 50 kHz being most common. Therefore, bats should be several times better at avoiding obstacles than one would expect from Example 6. This is not too surprising if the system is good enough to catch insects on the wing, which the bats must approach much closer than 1 meter.

Interestingly, bats appear to be rather economical in their use of pulses, using relatively long pulses (15 ms) at long repetition intervals when they are cruising far above the ground and relatively short pulses (1 ms) at short repetition intervals only when they are pursuing insect prey.

Many other characteristics of the bat echolocation system can be explained by an extension of the kinds of arguments given here. For example, theoretically one expects that the intensity of the returning echo from an object at a certain distance, should decrease with the size of the object. The echolocation system provides information about the size of objects in the environment from the intensity of the returning echo, and information about the distance of objects from the time delay between the emission of the pulse and the reception of the echo. However, the character of the echo should theoretically be relatively insensitive to the detailed nature of the object causing the echo, which perhaps explains the interest exhibited by bats in pebbles tossed in the air by small boys and naturalists.

In certain bats, for example those of the genus Rhinolophus, the Doppler effect appears to be the physical phenomena which is the key to an understanding of their system of echolocation (Schuller, et al. 1974). Several of the important considerations involved in the application of the Doppler effect to bats are developed in the following problem.

Problem 8

A bat is flying along at 5 m s^{-1}. It emits a 50 kHz sound pulse which is reflected by an insect which is 5 meters distant and is moving away at 1m s^{-1}. What is the frequency of the echo, and how long after the pulse begins does the echo begin to return?

Answer: f_L = 51.74 kHz

t = 28.6 ms

The outgoing and incoming frequencies in this example have a difference of 1740 Hz. This difference may appear quite large when compared to the difference between Concert A (440 Hz) and the A an octave higher (880 Hz). However, in the detection of radiation phenomena, the important comparison is the ratio, not the difference of two frequencies. The bat in Problem 8 must be able to detect 1740 Hz in 50 kHz, a percentage frequency change of 3.4%. This is not an unreasonable change to detect since human musicians can quite commonly distinguish quarter tones which represent a percentage frequency change of 3%. One expects that bats which depend upon the Doppler effect should have very acute pitch change detection and a very stable emission frequency, to go along with the ability to discriminate very small time intervals. Some of these predictions have been experimentally verified (Schuller, et al. op cit.).

The thrust of the discussion presented in this section is perhaps most striking when viewed in terms of the advantages and constraints that the utilization of echolocation has conferred on the evolution of the Chiroptera. The development of echolocation has allowed the bat to utilize a previously unexploited resource, night flying insects, but in turn has placed a premium on those bats that are able to emit high frequencies in short pulses, that can detect faint echoes, and that can detect relatively small shifts in frequency between outgoing and incoming pulses. The selection pressure for these attributes is the force responsible for numerous remarkable physical and behavioral adaptations. Our understanding of this system is by no means complete; echolocation remains a fertile territory for experiment and theory.

V. SUMMARY

The preceding discussion has presented some of the results from classical and modern radiation theory and demonstrated how these physical principles can be applied to the analysis of biological systems. The emphasis in these applications has been upon the evolutionary significance of the physical processes. In the biological applications presented, the physical processes are involved in the following two types of explanations.

In the first type of explanation, physical theory is used to isolate constant factors in the environment to which all organisms must adjust their evolution. The most striking example of this is that the wavelength been experimentally verified (Schuller, et al. op cit.).

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Weeg, G. P. and Reed, G. B. 1966. Introduction to Numerical Analysis. Blaisdell Publishing Co., Waltham, Massachusetts. 184 pp.

RADIATION

Appendix 1. Symbols, Units and Dimensions

Symbol	Quantity	Units	Dimension
α	angle	radians	---
b	Wien constant	2.8978×10^{-3} m K	$L\theta$
c	speed of light	2.998×10^{8} m s^{-1}	LT^{-1}
C_s	speed of sound	3.50×10^{2} m s^{-1}	LT^{-1}
D	distance	m	L
d	distance to an object	m	L
d_i	i^{th} difference term	---	---
$d\lambda$	differential wavelength	m	L
$d\nu$	differential frequency	s^{-1}	T^{-1}
$\delta\theta$	infinitesimal angle	radians	---
δx	infinitesimal distance	m	L
E[illegible]	total power	J s^{-1}	$ML^{2}T^{-3}$
E_E	power flow at earth's surface	J m^{-2} s^{-1}	MT[illegible]
E_n	radiation emittance	J m^{-2} s^{-1}	MT^{-3}
E_s	power flow at sun's surface	J m^{-3} s^{-1}	MT^{-3}
$E(\lambda)$	energy density as a function of wavelength	J m^{-4}	$ML^{-2}T^{-2}$
$E(\nu)$	energy density as a function of frequency	J m^{-3} s	$ML^{-1}T^{-1}$
e	base of natural logarithms	2.171828...	---
f_L	frequency at listener	s^{-1}	T^{-1}
f_s	frequency at source	s^{-1}	T^{-1}
H	total heat loss rate	J s^{-1}	$ML^{2}T^{-3}$

Appendix I (cont'd)

Symbol	Quantity	Units	Dimension
Hz	Hertz	s^{-1}	T^{-1}
h	Planck constant	6.626×10^{-34} J s	ML^2T^{-1}
k	Boltzmann constant	1.381×10^{-23} J K^{-1}	$ML^2T^{-2}\theta^{-1}$
λ	wavelength	m	L
λ_B	wavelength behind source	m	L
λ_F	wavelength in front of source	m	L
λ_m	wavelength at which black-body spectrum has maximum energy density	m	L
O	observer	---	---
R_i	i^{th} remainder term	---	---
r	radius	m	L
r_E	mean distance from earth to sun	[illegible]9 × 10^{11}m	L
r_s	radius of sun	7.1×10^8m	L
S	source	---	---
s_o	size of an object	m	L
SA	surface area	m^2	L^2
σ	Stefan-Boltzmann constant	5.6696×10^{-8} J s^{-1} m^{-2} K^{-4}	$ML^{-2}T^{-1}\theta^{-4}$
T	temperature	K	
	a particular time	s	T
T_a	ambient temperature	K	θ
T_o	temperature of organism	K	θ
T_s	surface temperature of sun	K	θ
t	time variable	s	T

Appendix 1 (cont'd)

Symbol	Quantity	Units	Dimension
u	actual solution	---	---
ν	frequency	s^{-1}	T^{-1}
V_L	listener velocity	$m\ s^{-1}$	$T^{-1}L$
V_s	source velocity	$m\ s^{-1}$	$T^{-1}L$
x_i	i^{th} trial solution	---	---
x_o	point in space corresponding to source position at $t = 0$	m	L
x_T	point in space corresponding to source position at $t = T$	m	L

L = length

M = mass

T = time

θ = temperature

Appendix 2: I. Numerical Techniques

Introduction

In the discussion of black-body radiation there arose two equations which could not be solved analytically. Since such equations arise not infrequently in a variety of areas, for example in mathematical modeling of biological systems, it is worthwhile to investigate methods by which one can find solutions to such equations. One class of such methods, called numerical techniques, utilizes the recursive application of the basic operations defined on the real number system (+, −, ×, ÷), to find solutions accurate to any desired accuracy. With the increased availability of machines which can carry out these techniques swiftly and automatically, the problem solving ability of the scientist has increased enormously. In this appendix, two important numerical techniques, successive approximation, and the half increment method for definite integrals, will be presented and their implementation on the increasingly ubiquitous programmable pocket calculator will be demonstrated.

Successive Approximation

As an example of this technique, the solution of the transcendental equation

$$e^{-u} + \frac{1}{5}u - 1 = 0 \qquad \text{(A-1)}$$

which arose in the discussion of Wien's Law will be discussed.

Here u is the unknown to be calculated. Suppose one starts with a trial solution x_1. If d_1 is the difference between the first trial solution x_1 and the actual solution u, then

$$x_1 = u - d_1.$$

Substituting x_1 for u in eq. (A-1) gives:

$$e^{-x_1} + \frac{1}{5}x_1 - 1 = R_1 \qquad \text{(A-2)}$$

where R_1 is the first remainder term. Clearly as $R_n \to 0$ the n^{th} trial solution x_n will approach u.

Subtracting eq. (A-1) from eq. (A-2) one obtains:

$$\left(e^{-x_1} - e^{-u_1} \right) - \frac{1}{5} d_1 = R_1$$

or

$$e^{-x_1}\left(1 - e^{-d_1}\right) - \frac{1}{5} d_1 = R_1 \qquad \text{(A-3)}$$

The exponential in the unknown d_1 in eq. (A-3) can be expanded as an infinite series (e.g., a Taylor series):

$$e^{-d_1} = 1 - d_1 + \frac{d_1^{\,2}}{2!} - \frac{d_1^{\,3}}{3!} + \frac{d_1^{\,4}}{4!} - \cdots\cdot\cdot$$

If the first trial solution is a reasonable guess then $|d_1|$ will be small so that the first few terms in the infinite series will dominate. Using only the first two terms, eq. (A-3) becomes:

$$e^{-x_1}(d_1) - \frac{1}{5} d_1 = R_1$$

or

$$d_1(e^{-x_1} - 1/5) = R_1$$

or finally:

$$d_1 = R_1 \Big/ (e^{-x_1} - 1/5) \qquad \text{(A-4)}$$

Clearly the second trial solution x_2, defined by

$$x_1 = u - d_1.$$

Substituting x_1 for u in eq. (A-1) gives:

$$e^{-x_1} + \frac{1}{5}x_1 - 1 = R_1 \qquad \text{(A-2)}$$

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$$e^{-d_1} = 1 - d_1 + \frac{d_1^{\ 2}}{2!} - \frac{d_1^{\ 3}}{3!} + \frac{d_1^{\ 4}}{4!} - \ldots\ldots$$

If the first trial solution is a reasonable guess then $|d_1|$ will be small so that the first few terms in the infinite series will dominate. Using only the first two terms, eq. (A-3) becomes:

$$\epsilon^{-x_1}(d_1) - \frac{1}{5} d_1 = R_1$$

or

$$d_1(e^{-x_1} - 1/5) = R_1$$

or finally:

$$d_1 = R_1 \Big/ (e^{-x_1} - 1/5) \qquad \text{(A-4)}$$

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If the first trial solution is a reasonable guess then $|d_1|$ will be small so that the first few terms in the infinite series will dominate. Using only the first two terms, eq. (A-3) becomes:

$$e^{-x_1}(d_1) - \frac{1}{5} d_1 = R_1$$

or

$$d_1(e^{-x_1} - 1/5) = R_1$$

or finally:

$$d_1 = R_1 \Big/ (e^{-x_1} - 1/5) \qquad \text{(A-4)}$$

Clearly the second trial solution x_2, defined by

TABLE A-1 (SR-52) Solution to $e^{-u} + \frac{1}{5}u - 1 = 0$

Register Contents:

00	01	02	03-18	19
—	x_i	R_i	—	Used for calculation of R_i' (SBR 1*)

Program:

Step	Code	Key Entry	Comments
000	42	STO	x_i in display
001	00	0	
002	01	1	x_i stored in register 01
003	51	SBR	
004	87	1*	Calculates R_i
005	42	STO	
006	00	0	
007	02	2	R_i stored in register 02
008	81	HLT	Cease execution, display R_i
009	43	RCL	
010	00	0	
011	01	1	Recall x_i
012	51	SBR	
013	23	ℓnx	Calculates e^{-x_i}
014	75	—	
015	93	.	
016	02	2	
017	95	=	$e^{-x_i} - \frac{1}{5}$ in display
018	20	1/x	$(e^{-x_i} - \frac{1}{5})$ in display
019	65	x	

(Continued)

Note 1* refers to 2nd 1.

TABLE A-1 (SR-52), Continued

Step	Code	Key Entry	Comments
020	43	RCL	
021	00	0	
022	02	2	Recall R_i
023	95	=	$d_i = R_i(e^{-x_i} - \frac{1}{5})^{-1}$ in display
024	85	+	
025	43	RCL	
026	00	0	
027	01	1	Recall x_i
028	95	=	$x_{i+1} = x_i + d_i$ in display
029	81	HLT	Cease execution, display x_{i+1}
030	86	rset	Return to step 000
031	46	LBL	
032	23	ℓnx	Subroutine ℓnx
033	94	+/-	
034	22	INV	
035	23	ℓnx	Calculate e^{-x_i}
036	56	rtn	
037	46	LBL	
038	87	1*	Subroutine 1*
039	53	(	
040	42	STO	
041	01	1	
042	09	9	Store x_i in register 19

(Continued) NOTE: 1* refers to 2nd 1.

TABLE A-1 (SR-52), Continued

Step	Code	Key Entry	Comments
043	51	SBR	
044	23	ℓnx	Calculate e^{-x_i}
045	75	-	
046	01	1	Calculate $e^{-x_i} - 1$
047	85	+	
048	53	(	
049	43	RCL	
050	01	1	
051	09	9	Recall x_i
052	55	÷	
053	05	5	Calculate $\frac{1}{5} x_i$
054	54	)	
055	54	)	Calculate R_i
056	56	rtn	

B. The HP-25

Using the Program (Table A-2):

Switch the PGRM-RUN switch to PGRM. Clear by keying f PGRM. Then key steps 01 through 24 of the program. Switch PGRM-RUN switch to RUN, and set the calculator to step 00 by keying f PGRM. Key x_1 into the display. Run the program by pushing the R/S button. The calculator will cease executing when R_1 has been calculated. R_1 will be in the (x) display. Push R/S; after calculation x_2 will be displayed. Push R/S; the display will show R_2, etc.

To try a different first trial solution, key f PGRM and then key in the new x_1. Run the program as before.

There are two solutions to eq. (A-1): u = 0.0 and u = 4.9651... If x_1 is too small or negative, this program will converge to the trivial solution (u = 0.0). Try a larger x_1; i.e., key f PGRM, and then key in the new x_1. Run the program as before. If x_1 is too large, the display will show OF when the calculator ceases execution. Start over again with a smaller x_1.

For troubleshooting and editing of a HP-25 program, see section IV.B. of this appendix.

TABLE A-2 (HP-25). Solution to Transcendental Equation

Register	Contents
0-7	0

Step	Code	Key	X	Y	Z	T	Comment
00							x_1 in display
01	23 01	STO1	x_1				Start loop
02	31	ENTER	x_1	x_1			
03	32	CHS	$-x_1$	x_1			
04	15 42	g e^x	e^{-x_1}	x_1			
05	31	ENTER	e^{-x_1}	e^{-x_1}	x_1		
06	31	ENTER	e^{-x_1}	e^{-x_1}	e^{-x_1}	x_1	
07	73	•	•	e^{-x_1}	e^{-x_1}	x_1	
08	02	2	.2	e^{-x_1}	e^{-x_1}	x_1	
09	32	CHS	-.2	e^{-x_1}	e^{-x_1}	x_1	
10	51	+	$e^{-x}-.2$	e^{-x_1}	x_1	x_1	
11	23 02	STO2	$e^{-x_1}-.2$	e^{-x_1}	x_1	x_1	
12	22	R↓	e^{-x_1}	x_1	x_1	$e^{-x_1}-.2$	
13	21	$x \gtrless y$	x_1	e^{-x_1}	x_1	$e^{-x_1}-.2$	

(Continued)

TABLE A-2 (HP-25). Continued

Step	Code	Key	X	Y	Z	T	Comment
14	31	ENTER	x_1	x_1	e^{-x_1}	x_1	
15	05	5	5	x_1	e^{-x_1}	x_1	
16	71	÷	$1/5\ x_1$	e^{-x_1}	x_1	x_1	
17	31	ENTER	$1/5\ x_1$	$1/5\ x_1$	e^{-x_1}	x_1	
18	01	1	1	$1/5\ x_1$	e^{-x_1}	x_1	
19	41	-	$1-1/5\ x_1$	e^{-x_1}	x_1	x_1	
20	51	+	R_1	x_1	x_1	x_1	Calculate R_1
21	74	R/S	R_1	x_1	x_1	x_1	Display R_1
22	24 02	RCL2	$e^{-x_1}-.2$	R_1	x_1	x_1	
23	71	÷	d_1	x_1	x_1	x_1	Calculate d_1
24	24 01	RCL1	x_1	d_1	x_1	x_1	
25	51	+	x_2	x_1	x_1	x_1	Calculate x_2
26	74	R/S	x_2	x_1	x_1	x_1	Display x_2
27	13 01	GTO 01	x_2	x_1	x_1	x_1	

C. Using Successive Approximation to Solve Other Problems

The method of successive approximation is a powerful technique for finding the solution to certain equations quickly and easily, as illustrated by the programmed solution to eq. (A-1). Besides transcendental equations (viz. (A-1)), this technique is useful for solving:

1) Polynomials with constant coefficients of any degree
2) Polynomials with variable coefficients of small degree.

The crux of the method is finding an explicit formula for a correction term (d_i) so that from any trial solution (x_i) one can calculate a new solution (x_{i+1}) which is a better approximation to the correct solution than the original (x_i). To find this correction formula often strains the ingenuity of the problem solver, who may have to juggle equations or approximate functions by series. A particularly useful method for finding these correction formulae, especially for the polynomial problems listed above, is the Newton-Raphson method which is derived and discussed in almost all introductory books on numerical methods[1].

Definite Integrals by the Half-Increment Method

In the derivation of the Stefan-Boltzmann law, it was necessary to evaluate the indefinite integral:

$$\int_0^\infty \frac{x^3}{e^x-1}\,dx. \qquad \text{(A-5)}$$

[1][see, e.g., Weeg & Reed 1966, p. 34.]

This seemingly simple integral cannot be evaluated analytically. Unfortunately, this is not an isolated example. That is, the majority of functions, including many important simple functions, cannot be integrated by standard analytical techniques. In such cases, one must resort to numerical methods to obtain the desired integral. The particular numerical integration technique described in this appendix, the half-increment method, is simple to understand and to implement on a programmable pocket calculator, and has the added advantage of (relatively) rapid convergence.

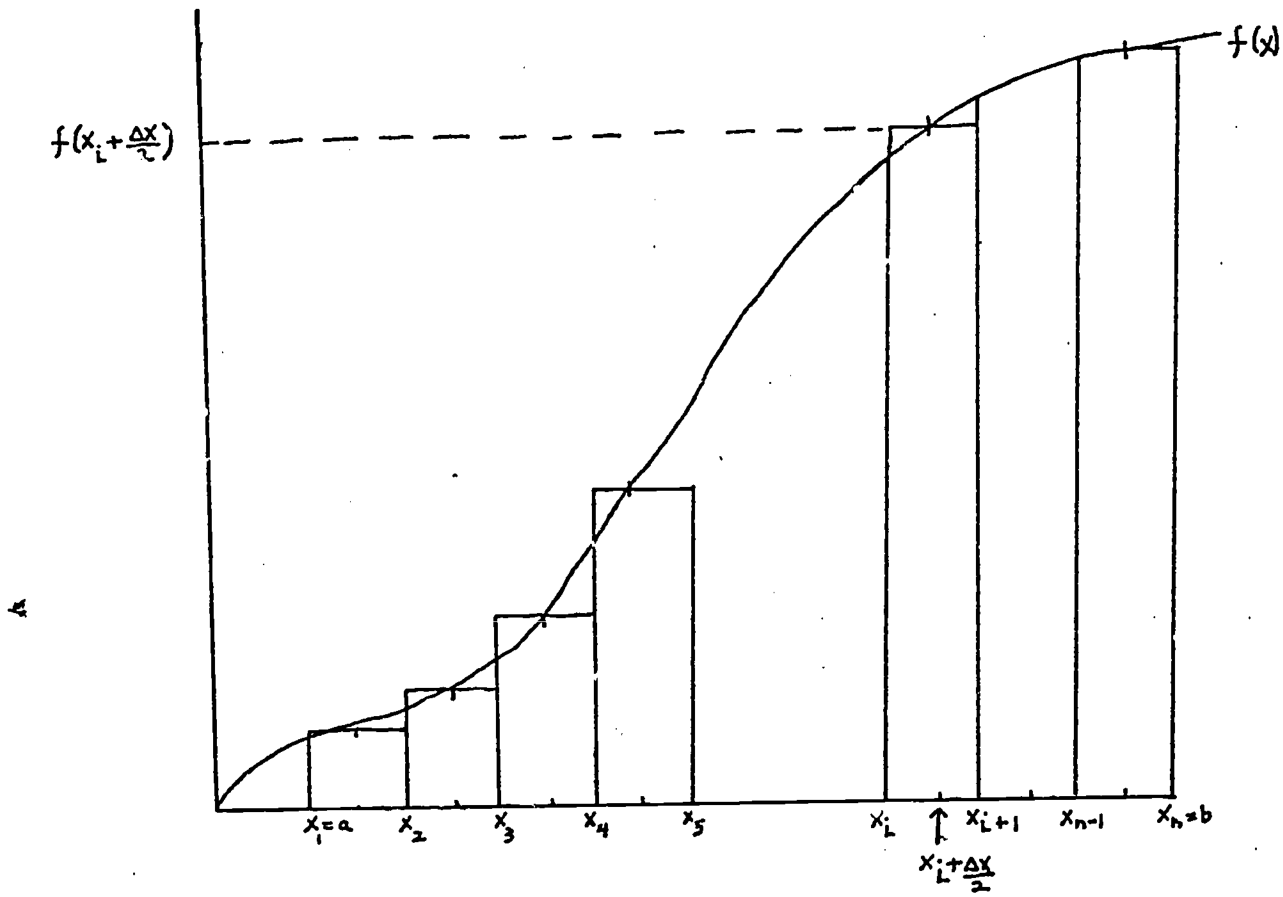
In elementary calculus, one learns that an integral can be thought of as a measure of an area. For a definite integral such as:

$$\int_a^b f(x)dx \qquad \text{(A-6)}$$

this area is defined by the curve of the function to be integrated, $f(x)$, the x-axis, and the vertical lines $x = a$ and $x = b$. This area can be approximated by the sum of the area of rectangles as illustrated in Figure A-1. The thinner the rectangles and thus the greater the number of rectangles, the more accurate the approximation. In fact, it can be shown that in the limit as the width of the rectangles becomes infinitesimal ($\Delta x \to 0$ in Fig. A-1), the value of the sum approaches the value of the integral.

All numerical integration techniques are based on approximating an integral by the sum of the areas of simple plane figures. This particular method is called the half-increment method because the height of each rectangle is determined by the value of the function at the x value which is half-way between the two x values which define the vertical boundaries of the rectangle. That is, for the i^{th} rectangle, whose vertical

Figure A-1. Definite integral approximated by rectangles



The value of the integral, that is the area under the curve f(x) from x = a to x = b, is approximated by the sum of the area of the rectangles illustrated above. In this approximation, the height of each rectangle is taken to be the value of the function at the x value halfway from the endpoints of the rectangle.

boundaries are determined by $x = x_i$ and $x = x_{i+1} = x_i + \Delta x$, the height of the rectangle is given by $f(x_i + \frac{\Delta x}{2}) = f(x_{i+1} - \frac{\Delta x}{2})$.

In the programs that follow, the integral (A-6) is evaluated first as a sum of rectangles whose width, $\Delta_1 x$, is given by $\Delta_1 x = b - a$. This sum, Σ_1, which is composed of only one term, is given by:

$$\Sigma_1 = f\left(a + \frac{\Delta_1 x}{2}\right) \Delta_1 .$$

Next the sum, Σ_2, is calculated for $\Delta_2 x = \frac{\Delta_1 x}{2}$. At each succeeding iteration, the width of the rectangles is halved; that is:

$$\Delta_{i+1} x = \frac{1}{2}\Delta_i x$$

and

$$\Sigma_i = \sum_{j=1}^{2^i} f\left(x_j + \frac{\Delta_i x}{2}\right)\Delta_i x$$

where

$$x_1 = a \quad \text{and} \quad x_{2^i} = b.$$

When the value of the sum as determined by two successive iterations is the same, this sum is taken to be the value of the integral. Obviously, each iteration will require twice as many operations as the preceding, and will take correspondingly longer.

The integral of interest, (A-5), is indefinite, although the method as presented is only applicable to definite integrals. Fortunately, the sum does not have to be evaluated for very large b (the upper limit in (A-6)) in order to be accurate to two decimal places. This is a result of the following limits:

$$\lim_{x \to 0} \frac{x^3}{e^x - 1} = \lim_{x \to \infty} \frac{x^3}{e^x - 1} = 0$$

(which can be calculated by L'Hospital's rule), and the fact that the function approaches zero very quickly (and monotonically) for sufficiently large x.

A. The SR-52

Using the program (Table A-3):

With the calculator in the execute mode, key LRN to enter programming mode. Key in steps 000-111. Key LRN to return to the execute mode. Push rset to go to step 000. Load the value of a in register 01 (i.e., key in the value of a, and push STO 01,), and the value of b in register b. Push RUN. When the calculator ceases execution of the program, Σ_1 will be displayed. Push RUN. Σ_2 will be displayed, and Σ_1 will be in register 06. Run the program until $\Sigma_i = \Sigma_{i-1}$ (Σ_i will be in register 05, Σ_{i-1} will be in register 06). Note that each iteration takes twice as long as the preceding one.

Clearly the lower limit of the sum should be taken as the same as the lower limit of the integral (A-5); that is, a = 0.0. However, the upper limit (b) is not as easy to choose. The larger the value of b, the better the approximation of the sum to the integral. However, concomitant with a larger b is a greater number of iterations required for convergence. A good compromise value is b = 30, which will approximate the actual value of the integral (I = 6.4938...) to 3 decimal places in 9 iterations. The program user should try other (larger and smaller) values of b in order to get some feeling for these tradeoffs.

For troubleshooting and editing of an SR-52 program, see Section IV.A of this appendix.

TABLE A-3 (SR-52). Integral by Half-increment Method

Register Contents

00	01	02	03	04	05	06	07 - 18	19
—	$\underbrace{a \quad b}_{\text{preloaded}}$		x_i	Δx	Σ	I_{i-1}	—	used for f(x)

Program

Step	Code	Key Entry	Comments
000	00	0	
001	42	STO	
002	00	0	
003	05	5	Zero register 05
004	43	RCL	
005	00	0	
006	02	2	Recall b
007	75	−	
008	43	RCL	
009	00	0	
010	01	1	Recall a
011	42	STO	
012	00	0	
013	03	3	Store x_1 = a in Register 03
014	95	=	Calculate $\Delta_1 x$ = b-a
015	42	STO	
016	00	0	
017	04	4	Store $\Delta_1 x$ in Register 04

(Continued)

TABLE A-3 (SR-52), Continued

Step	Code	Key Entry	Comments
018	55	÷	
019	02	2	
020	95	=	Calculate $\frac{\Delta x}{2}$
021	85	+	
022	43	RCL	
023	00	0	
024	03	3	Recall x_i
025	95	=	Calculate $x_i + \frac{\Delta x}{2}$
026	51	SBR	
027	00	0	This subroutine
028	09	9	calculates
029	05	5	$f\ (x_i + \frac{\Delta x}{2})$
030	65	x	
031	43	RCL	
032	00	0	
033	04	4	Recall
034	95	=	Calculate $f(x_i + \frac{\Delta x}{2})\ \Delta x$
035	44	SUM	Put
036	00	0	$\sum_{x_1=a}^{x_i} f(x_i + \frac{\Delta x}{2})\ \Delta x$ in
037	05	5	Register 05
038	43	RCL	
039	00	0	

(Continued)

TABLE A-3 (SR-52), Continued

Step	Code	Key Entry	Comments
040	04	4	Recall Δx
041	44	SUM	Calculate
042	00	0	$x_{i+1} = x_i + \Delta x$
043	03	3	Store in Register 03
044	43	RCL	
045	00	0	
046	03	3	Recall x_{i+1}
047	75	-	
048	43	RCL	
049	00	0	
050	02	2	Recall b
051	95	=	Calculate $x_{i+1} - b$
052	80	if pos	If $x_{i+1} > b$ go to
053	32	sin	step labeled sin
054	43	RCL	If $x_{i+1} < b$
055	00	0	Recall
056	04	4	Δx
057	41	GTO	Continue
058	00	0	the sum
059	01	1	
060	08	8	

(Continued)

TABLE A-3 (SR-52), Continued

Step	Code	Key Entry	Comments
061	46	LBL	
062	32	sin	
063	43	RCL	
064	00	0	
065	05	5	Recall Σ
066	81	HLT	Display Σ
067	43	RCL	
068	00	0	
069	05	5	Recall Σ
070	42	STO	
071	00	0	
072	06	6	Store Σ in Register 06
073	00	0	
074	42	STO	
075	00	0	
076	05	5	Zero Register 05 (Σ)
077	02	2	
078	22	INV	
079	49	PROD	
080	00	0	Put $\Delta_{i+1}x = \frac{\Delta_i x}{2}$ in
081	04	4	Register 04
082	43	RCL	
083	00	0	

continued

TABLE A-3 (SR-52), Continued

Step	Code	Key Entry	Comments
084	01	1	Recall a
085	42	STO	
086	00	0	
087	03	3	Store x_1 = a in Register 03
088	43	RCL	
089	00	0	
090	04	4	Recall $\Delta_{i+1}x$
091	41	GTO	Return to Step 018
092	00	0	to recalculate
093	01	1	Integral w/ Smaller
094	08	8	Δx
095	42	STO	Store
096	01	1	$x_i + \frac{\Delta x}{2}$ in
097	09	9	Register 19
098	45	Y^x	
099	03	3	Calculate $\left(x_i + \frac{\Delta x}{2}\right)$
100	55	÷	
101	53	(	
102	43	RCL	
103	01	1	
104	09	9	Recall $\left(x_i + \frac{\Delta x}{2}\right)$
105	22	INV	
106	23	ℓnx	Calculate $\exp\left(x_i + \frac{\Delta x}{2}\right)$

continued

TABLE A-3 (SR-52), Continued

Step	Code	Key Entry	Comments
107	75	-	
108	01	1	
109	54	)	Calculate $\exp\left(x_i + \frac{\Delta x}{2}\right) - 1$
110	95	=	Calculate $f\left(x_i + \frac{\Delta x}{2}\right)$
111	56	rtn	

B. The Ḧ ..5

Using the program (Table A-4):

Switch the PGRM-RUN switch to PGRM. Clear program memory by pushing f PGRM. Then key in steps 01 through 46 of the program. Switch PGRM-RUN switch to RUN, and set the calculator to step 00 by keying f PGRM. Load a in register 1 (i.e., key a into the display then push STO 1) and b in register 2. Push R/S. The display will show Σ_1. Push R/S. The display will show Σ_2. Σ_1 will be in register 6. Run the program until Σ_i (in the display at the end of execution and in register 5) equals Σ_{i-1} (in register 6). Note that each iteration takes about twice as long as the previous one.

Clearly the lower limit of the sum should be the same as the lower limit of the integral (A-5); i.e., a = 0.0. However, the upper limit of the sum (b) is not as easy to choose. The larger the value of b, the better the approximation of the sum to the integral, but the longer it takes for two successive iterations to converge. A good compromise value is b = 30, which will approximate the actual value of the integral (I = 6.4938...) to three decimal places in nine iterations. The program user should try other (larger and smaller) values of b in order to get some feeling for the tradeoff between accuracy and time in using this method on this integral.

For troubleshooting and editing of an HP-25 program see section IV.B of this appendix.

TABLE A-4 (HP-25) $\int_a^b \frac{x^3}{e^x-1}\,dx$ by Half-Increment Method

Register Contents

0	1	2	3	4	5	6	7
-	a	b	x_i	Δx	Σ	Σ_{i-1}	-
	preloaded						

Program:

Step	Code	Key Entry	X	Y	Z	T	Comments
01	00	0	0				
02	23 05	STO 5	0				Zero register 5
03	24 02	RCL 2	b				Recall b
04	24 01	RCL 1	a	b			Recall a
05	23 03	STO 3	a	b			
06	41	-	$\Delta_1 x=b-a$				Calculate $\Delta_1 x=b-a$
07	23 04	STO 4	Δx				
08	02	2	2	Δx			Continue loop [from step 36]
09	71	÷	$\Delta x/2$				Calculate $\Delta x/2$
10	24 03	RCL 3	x_i	$\Delta x/2$			
11	51	+	$x_i+\Delta x/2$				Calculate $x_i+\Delta x/2$

(Continued)

BLE A-4 (HP-25), Continued

ep	Code	Key Entry	X	Y	Z	T	Comments
	31	ENTER	$x_i+\Delta x/2$	$x_i+\Delta x/2$			Calculate $\exp[x_i+\Delta x/2]$
	15 07	ge^x	$\exp[x_i+\Delta x/2]$	$x_i+\Delta x/2$			
	01	1	1	$\exp[x_i+\Delta x/2]$	$x_i+\Delta x/2$		
	41	-	exp[]-1	$x_i+\Delta x/2$			Calculate $\exp[x_i+\Delta x/2]$
	21	$x \gtrless y$	$x_i+\Delta x/2$	exp[]-1			
	31	ENTER	$x_i+\Delta x/2$	$x_i+\Delta x/2$	exp[]-1		
	03	3	3	$x_i+\Delta x/2$	exp[]-1		
	14 03	fy^x	$(x_i+\Delta x/2)^3$	exp[]-1			Calculate $(x_i+\Delta x/2)^3$
	21	$x \gtrless y$	exp[]-1	$(x_i+\Delta x/2)^3$			$(x_i+\Delta x/2)^3$
	71	÷	$f(x_i+\Delta x/2)$				$f(x_i+\Delta x/2) =$
							$(x_i+\Delta x/2)^3 \quad \exp[x_i+\Delta x/2]-1$
	24 04	RCL 4	Δx	$f(x_i+\Delta x/2)$			
	61	x	$f(x_i+\Delta x/2)\Delta x$				Calculate $f(x_i+\Delta x/2)\Delta x$
	23 51 05	STO+5	$f(x_i+\Delta x/2)\Delta x$				Sum of areas in reg. 5
	24 04	RCL 4	Δx	$f(x_i+\Delta x/2)$			
	24 03	RCL 3	x_i	Δx	$f(x_i+\Delta x/2)$		

ontinued)

Table A-4 (HP-25), Continued

Step	Code	Key Entry	X	Y	Z	T	Comments
27	51	+	$x_i+\Delta x$	$f(x_i+\Delta x/2)$			$x_{i+1} = x_i+\Delta x$
28	23 03	STO 3	x_{i+1}	$f(x_i+\Delta x/2)$			x_{i+1} in reg. 3
29	24 02	RCL 2	b	x_{i+1}	$f(x_i+\Delta x/2)$		Test for x_{i+1} beyond
30	14 41	fx<y	b	x_{i+1}	$f(x_i+\Delta x/2)$		range of integration
31	13 36	GTO 36	b	x_{i+1}	$f(x_i+\Delta x/2)$		of x_{i+1}>b, leave loop,
							go to step 36
32	24 04	RCL 4	Δx	b	x_{i+1}	$f(x_i+\Delta x/2)$	If $x_{i+1} < b$
33	31	ENTER	Δx	Δx	b	x_{i+1}	
34	13 08	GTO 08	Δx	Δx	b	x_{i+1}	Continue loop at step 08
35	24 05	RCL 5	Σ	b	x_{i+1}	$f(x_i+\Delta x/2)$	
36	74	R|S	Σ	b	x_{i+1}	$f(x_i+\Delta x/2)$	Cease execution, display Σ_i
37	23 06	STO 6	Σ	b	x_{i+1}	$f(x_i+\Delta x/2)$	$\Sigma_i \to \Sigma_{i-1}$ in reg. 6
38	24 01	RCL 1	a	Σ	b	x_{i+1}	
39	23 03	STO 3	a	Σ	b	x_{i+1}	x_1 = a in reg. 3
40	14 34	f STK	0	0	0	0	Zero stack
41	25 05	STO 5	0				Zero reg. 5

(continued)

TABLE A-4 (HP-25), Continued

Step	Code	Key Entry	X	Y	Z	T	Comments
42	02	2	a				lower limit from reg 2
43	23 71 04	STO÷4	2				$\Delta_{i+1}x \leftarrow \frac{\Delta_i x}{2}$ in reg. 4
44	24 04	RCL 4	Δx	2			
45	21	$x \gtrless y$	2	Δx			
46	13 09	GTO 09	2	Δx			Recalculate sum with smaller rectangles

C. Using the Half-Increment Method to Integrate Other Functions[1].

The SR-52:

The subroutine 095 calculates the value of $f(x_i + \frac{\Delta x}{2})$. To integrate any other function, define the function with suitable keystrokes starting at program step 095 Be sure to end the function definition subroutine with rtn.

If the program is already loaded into program memory it is possible to change only those statements involved in the functional definition (subroutine 095), which is usually less trouble than wiping program memory and starting anew. For appropriate editing instructions, see section II.A of this appendix.

The HP-25:

The steps 12 through 22 are used to calculate the value of $f(x_i + \frac{\Delta x}{2})$. To integrate any other function, define the function with suitable key strokes starting at step 12. Be sure to end the sequence with $f(x_i + \frac{\Delta x}{2})$ in the X register. Follow the last step used to define the function with the step numbered 23 in the present program (that is, the keystrokes RCL 4).

If the program is already loaded into program memory, it is possible to change only those keystrokes involved in the functional definition (steps 12-22). This is usually less trouble than wiping program memory and starting anew. For appropriate editing instructions see Section II.B of this appendix.

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[1] [For alternative programs and more detailed discussion, see Eisberg, R. M. 1976.]

Appendix 2: II. Program Troubleshooting and Editing

It is frequently the case that after a program has been keyed into a calculator, the program will not perform as expected. This frustrating state of affairs may be due to a logical error in the program or mistakes made when keying in the program; e.g., leaving out steps, putting in extra steps, or keying steps in the incorrect order. Since such mistakes are relatively common, the design of programmable pocket calculators is such that troubleshooting and editing programs is not difficult.

Mistakes involving logical errors, which are the most difficult to detect, will not be present in the programs presented here. For such errors in your own programs, I have found that "single-stepping" through the programmed calculations (as described below) is the most efficient method of detecting the error. For further information, refer to the owner's handbook supplied with the calculator.

For nonlogical programming errors, there is always the option of wiping the program memory (usually by turning the machine off) and starting over. This procedure, besides being time consuming, does not assure that additional errors will not be made in loading the program the second time. Alternatively, one can edit the program as described below. In the following discussion, it is assumed that the program is already loaded into program memory.

A. The SR-52

Troubleshooting:

Programming errors are indicated by any of three conditions following a program RUN:

1) The calculator does not cease execution in a "reasonable" length of time. This condition is due to a closed loop in the program instructions. The calculator cannot exit the loop so as to reach a HLT instruction.

2) When the program ceases executing, the display is steady, but the answer is clearly incorrect. This situation may be difficult to detect unless one knows exactly what the program does.

3) When the program ceases executing, the display is flashing. This condition signifies that during execution, a calculation was performed that overflowed the capacity of the calculator, or that an illegal operation was performed.

There are two methods by which to pinpoint the source of an error. One can check the program in the memory against the program listing, or one can single-step manually through the calculations that the calculator performs automatically.

To check the program in the memory, push rset and then LRN to enter programming mode. The display will show the key code and step number of step 000. Pushing SST will display the key code and step number of the next step. Pushing bst will display this information for the preceding step. Compare the key codes displayed to those given in the program listing. If there is some reason to believe that the error occurs at some particular step, e.g., Step 099, one can go immediately to this step in the execute mode by pushing GTO 099. Then push LRN to enter the programming mode and to display the key code and step number 099. Use SST and bst as necessary.

Alternatively, one can single step through the programmed calculation manually. This is particularly useful for debugging your own programs or when a flashing display is encountered. In the execute mode, push rset to get to step 000. Load the registers and display as necessary. Continue in the execute mode and push SST. The calculator will execute instruction 000 and move on to the next step. Pushing SST repeatedly, one can observe the result of each programmed instruction as it is performed. If at any step an error condition results, push LRN to enter programming mode, and then push bst. The step number and key code of the incorrect step will be displayed.

Editing:

Deleting instructions: In the program mode, with the step number and key code of the incorrect step displayed, press del. The incorrect instruction will be deleted and the next instruction will be shifted down to this step number, and all subsequent instructions will shift down one step number.

Changing instructions: In the program mode, with the step number and key code of the incorrect step displayed, press the correct key for that stepnumber. The correct instruction will write over the previous one, and the display will shift to the next step.

Adding instructions: In the program mode with the step number and key code of the step displayed, press INS. The display will change to the correct step number but the key code will be 00. The key code that was at this step will be shifted to the next step number, as will all subsequent instructions. Press the key for the missing instructions. The display will now show the step number and key code of the next step.

B. The HP-25.

Troubleshooting:

Programming errors are indicated by any of four conditions following a program run:

1) The calculator does not cease execution after a "reasonable" length of time. This condition is due to a closed loop in the program instructions. The calculator cannot exit the loop so as to reach a R|S instruction.

2) When the program ceases executing, the answer displayed is clearly incorrect. This situation is difficult to detect.

3) When the program ceases executing ERROR is displayed. This results from attempting an illegal instruction. The program stops at the incorrect instruction, which will be displayed by switching to PGRM mode.

4) When the program ceases executing, OF is displayed. This results from an overflow in a storage register. Switch to PGRM mode to display the key code and step number of the instruction that caused this condition.

To compare the program in memory to the program listing, in the RUN mode push GTO 00 (or if there is reason to believe the error is at some later step, e.g., step 16, push GTO 16. Pushing SST will display the step number and key code of this step. When SST is released, the instruction is executed, the result is displayed, and the calculator moves on to the next step.

Editing:

Changing an instruction. Once the error is located, use the GTO (in RUN mode), the SST, or the bst (in PGRM mode) as necessary so as to be at the step preceding the step which is to be changed. In the PGRM mode, with the key code and step number of the preceding step displayed push the key of the correct instruction.

Deleting an instruction: Display the step preceding the step to be deleted (using GTO, SST, or bst as necessary). In the PGRM mode press g NOP. When the calculator reaches this program step, it will skip it and proceed to the next instruction.

Adding instructions: To add instructions, one uses the GTO instruction to perform an unconditional branching. For example, suppose one has left out three steps between Step 08 and 09. Further, suppose the program ends with Step 15. Then one replaces Step 08 with GTO 16. Then key in the instruction which was replaced at Step 08 in Step 16, and the three missing instructions as 17, 18, and 19. Then key in GTO 09 as Step 20.

CALCULATOR PROBLEMS

1. Using black and white infrared film and a suitable filter one can photograph within the wavelength range 500-650 nm. If you were to attempt to photograph the reindeer in problem 3 (main text), how much power would be reflected in these wavelengths by a m^2 of:

   a) The reindeer horn at T = 32°C?

   b) The outside of the reindeer's fur at T = 5°C?

   c) The external environment at T = 5°C?

   At present, infrared film is not "fast" enough to record thermal luminescence of an object at temperatures below 250°C.

   d) How much power would be available in this wavelength range from a black body at this temperature?

   The solution to this problem will require the numerical integration of

$$I = 3.74 \times 10^{-16} \int_{5\times10^{-7}}^{6.5\times10^{-7}} {}^{-5}[e^{hc/\lambda kT} - 1]^{-1} d\lambda$$

which can be derived in a manner analogous to the derivation of Eq. 1 but beginning with the solution to problem 1 (main text), that is

$$E(\lambda) = \frac{8\Pi hc}{\lambda^5} [e^{hc/\lambda kT} - 1]^{-1}.$$

2. The sensitivity of the compound eye of a honeybee (worker) extends further into the ultraviolet than does the sensitivity of the human eye. The bee eye is sensitive from about 300-650 nm, and the human eye is sensitive from about 400-700 nm. What is the difference in the power available from the sun in the wavelengths perceptible to these two organisms?

The solution to this problem will require the numerical integration of:

$$I = 3.74 \times 10^{-16} \int_b^a \lambda^{-5} \left[e^{2.52\times10^{-6}/2_1}\right]^{-1}$$

with the limits of integration chosen to coincide with the spectral ranges provided above.

What is the biological significance of the greater ultraviolet sensitivity of the bee eye?

3. Photosynthetic bacteria differ from most algae and higher plants in that they possess an auxiliary "electron pump" in their photosynthetic [illegible] which allows them to utilize radiation of longer wavelengths for photosynthesis. The absorption spectra for the photosynthetic organs of these organisms reveal the following spectral ranges:

a)	400–700 nm	green plants
b)	780–840 nm	various purple bacteria
c)	840–910 nm	various purple bacteria
d)	970–1050 nm	various purple bacteria

Using the integral in problem 2 above, calculate the power available from the sun in each of these wavelength ranges.

For an enlightening discussion of the evolutionary significance of the wavelength ranges utilized by these bacteria, see Björn 1976 (p. 235).

CALCULATOR PROBLEM SOLUTIONS

1. The integral to be evaluated is

$$I = 3.74 \times 10^{-16} \int_{5\times10^{-7}}^{6.5\times10^{-7}} \lambda^{-5}[e^{hc/\lambda kT} - 1]^{-1} d\lambda.$$

For the four parts of this problem the value of T differs, which means that the exponent of the exponential of the integral will be different for each part.

a) $T = 305°K$; $\frac{hc}{kT} = 4.718 \times 10^{-5}$

b) $T = 278°K$; $\frac{hc}{kT} = 5.1757 \times 10^{-5}$

c) $T = 268°K$; $\frac{hc}{kT} = 5.3688 \times 10^{-5}$

d) $T = 523°K$; $\frac{hc}{kT} = 2.751 \times 10^{-5}$.

For the SR-52:

As explained in section C of Appendix 2.II, one must alter the program in Table A-3 at step 095 which is the function defining subroutine. A suitable program is given in Table A-5. The preloaded registers in Table A-5 are 01, 02, and 07. Register 07 requires the values of hc/kT given above. Note that the value of the integral calculated by the program must be multiplied by 3.74×10^{-16} to give the correct value for the power.

For the HP-25:

As explained in section C of this appendix, one must alter the program in Table A-4 at step 12. A suitable program is given in Table A-6. The preloaded registers are 1, 2 and 7. Register 7 requires the values of hc/kT given above. Note that the value of the integral calculated by the program must be multiplied by 3.74×10^{-16} to give the correct value for the power.

The values for the integral that I obtained were:

a) $I = 2.41 \times 10^{-9}$

b) $I = 2.56 \times 10^{-12}$

c) $I = 9.45 \times 10^{-14}$

d) $I = 6.01 \times 10^{-4}$

Table A-5 (SR-52) Program Changes to Table A-3

00	01	02	03	04	05	06	07	08-18	19
--	5.7×10^{-7}	6.5×10^{-7}	x_i	Δx	Σ	I_{i-1}	$\frac{hc}{kT}$	----	used for f(x)
	preloaded						preloaded		

Step	Code	Key Entry	Comments
095	42	STO	Store
096	01	1	λ_i in
097	09	9	Register 19
098	45	Y^X	
099	05	5	
100	65	x	Calculate λ_i^5
101	53	(	
102	53	(	
103	43	RCL	
104	00	0	
105	07	F	Recall hc/kT
106	55	f	
107	43	RCL	
108	01	1	
109	09	9	Recall λ_i
110	54	)	Calculate $hc/\lambda kT$
111	22	INV	
112	23	$\ell n x$	Calculate $\exp[hc/\lambda kT] - 1$
113	75	-	
114	01	1	
115	54	)	Calculate $\lambda^5[\exp hc/\lambda kT-1]$

00	01	02	03	04	05	06	07	08–18	19
—	5.7×10^{-7}	6.5×10^{-7}	X_i	Δx	Σ	I_{i-1}	$\frac{hc}{kT}$	----	used for f(x)
	preloaded						preloaded		

Step	Code	Key Entry	Comments Comments
116	95	=	Calculate $\lambda^{-5}[\exp hc/\lambda kT-1] - 1$
117	20	1/x	Calculate $\lambda_i^{-5}[\exp(hc/kT)-1]^{-1}$
118	56	rtn	

Table A-6 (HP-25) Program Changes to Table A-4

Register Contents

0	1	2	3	4	5	6	7
-	a	b	x_i	Δx	Σ	Σ_{i-1}	hc/kT ↑
	preloaded						preloaded

Step	Code	Key Entry	X	Y	Z	T	Comments
12	31	ENTER	λ_i	λ_i			
13	31	ENTER	λ_i	λ_i	λ_i		
14	05	5	5	λ_i	λ_i		
15	14 03	fy^x	$(\lambda_i)^5$	λ_i	λ_i		Calculate λ_i^5
16	21	$x \lessgtr y$	λ_i	λ_i^5			
17	24 07	RCL 7	hc/kT	λ_i	λ_i^5		Recall hc/kT
18	21	$x \lessgtr y$	λ_i	hc/kT	λ_i^5		Calculate hc/λkT
19	71	÷	hc/λkT	λ_i	λ_i^5		Calculate hc/λkT
20	15 07	ge^x	exp[hc/λkT]	λ_i^5	λ_i^5		Calculate exp[hc/λk
21	01	1	1	exp[]	λ_i^5		
22	41	-	exp[]-1	λ_i^5			Calculate exp[hc/λk
23	61	x					
24	15 22	$g\frac{1}{x}$	$[\exp[-]]^{-1}$	λ_i^{-5}			Calculate $[\exp(\frac{hc}{\lambda kT})$
25	24 04	RCL 4	Δx	$f(x_1 + \frac{\Delta x}{2})$			Step No. 23 in Table A-4

Continue with steps 26-33 as in steps 23-30 in Table A-4

For this program, Step 31 Table A-4 must be changed to:

34 13 38 GTO 38.

Continue with steps 35-49 as in steps 32-46 in Table A-4.

2. The integral to be evaluated is the same as in problem 1. Thus one can use the programs given in Table A-5 (or A-6) preloading register 07 (or 7) with:

$$\frac{hc}{kT} = 2.52 \times 10^{-6}.$$

The value for the integral that I obtained was

a. 300-650 nm: $I = 6.38 \times 10^{22}$

b. 400-700 nm: $I = 5.85 \times 10^{22}$

3. The integral to be evaluated is the same as in problem 2. The values that I obtained for the different ranges of integration were

a. 400- 700 nm: $I = 5.85 \times 10^{22}$

b. 780- 810 nm: $I = 8.02 \times 10^{21}$

c. 840- 910 nm: $I = 8.123 \times 10^{21}$

d. 970-1050 nm: $I = 6.85 \times 10^{21}$

Appendix 3: SOLUTIONS TO PROBLEMS

Problem 1

Planck's formula in terms of λ:

$E(\nu) = 8\pi h\nu^3/c^3\ (e\ h\nu/kT - 1)^{-1}$.

So $E(\lambda)d\lambda = -E(\nu)d\nu$ (minus sign because $d\lambda$ and $d\nu$ are of opposite sign).

Since $V = c/\lambda$ for all wave phenomena,

$d\nu/d\lambda = -c/\lambda^2$.

$$\therefore \quad E(\lambda) = E(\nu)\ d\nu/d\lambda = E(\nu)\ e/\lambda^2$$
$$= c/\lambda^2 \left(\frac{8\pi h\nu^3}{c^3}\right)[e\ h\nu/kT - 1]^{-1}$$
$$= c/\lambda^2 (8\pi h/\lambda^3)[e^{hc/\lambda kT} - 1]^{-1}$$
$$= (8\pi hc/\lambda^5)[e^{hc}/\lambda T - 1]^{-1}.$$

Problem 2

The general formula is

$\lambda_m T = b$ or $\lambda_m = b/T$. So

a) $$\lambda_m = \frac{2.8978 \times 10^{-3}\text{m K}}{5.7 \times 10^3\ \text{K}} = 5.08 \times 10^{-7}\text{m}$$

b) Since 37°C = 300 K

$$\lambda_m = \frac{2.8978 \times 10^{-3}\text{m K}}{3 \times 10^2\ \text{K}} = 9.659 \times 10^{-4}\text{m}$$

c) Since 10°C = 283 K

$$\lambda_m = \frac{2.8978 \times 10^{-3}\text{m K}}{2.83 \times 10^2\ \text{K}} = 1.024 \times 10^{-3}\text{m}$$

d) Since -33°C = 240 K,

$$_m = \frac{2.898 \times 10^{-3} m\ K}{2.4 \times 10^2\ K} = 1.207 \times 10^{-3} m.$$

Problem 3

As in example 2

a) $E = \sigma\left[T_o^{\ 4} - T_a^{\ 4}\right] = 5.67 \times 10^{-8}\left[(273 + 32)^4 - (273 - 10)^u\right] W\ m^{-2}$

$= 219.4\ W\ m^{-2}$

$H = E(SA) = 219.4\ W\ m^{-2}(.1\ m^2) = 21.9$

b) $E = \sigma\left[T_o^{\ 4} - T_a^{\ 4}\right] = 5.67 \times 10^{-8}\left[(305)^4 - (228)^4\right] W\ m^{-2}$

$= 337.4\ W\ m^{-2}$

$H = E(SA) = 337.4(7.5 \times 10^{-3}) = 25.3\ W.$

Problem 4

$$E_E = \sigma T^u r_s^{\ 2}/r_c^{\ 2} = 5.67 \times 10^{-8}(5.70 \times 10^3)^4 \frac{(7.1 \times 10^8)^2}{(1.49 \times 10^{11})^2} W\ m^{-2}$$

$= 1.359 \times 10^3\ W\ m^{-2}.$

Converting to calories

$$E_E = 1.359 \times 10^3\ W\ m^{-2} = 1.359\ Wm^{-2}\left[.0239^{cal}/J\right]\left[\frac{60\ sec}{min}\ 10^{-4} m^2/cm^2\right]$$

$= 1.95\ cal\ min^{-1}\ cm^{-2}.$

Problem 5

As in Example 4:

$\alpha = 0.61\ \lambda/r$

$\lambda = 5.08 \times 10^{-7} m$

$r = 1.0\ mm = 1.0 \times 10^{-4} m$

So $\alpha = 3.17 \times 10^{-4}$ rad.

Again as in Ex. 4,

$$\delta x = \alpha d = (3.17 \times 10^{-4} \text{ rad})(17 \text{ mm})$$

$$\delta x = 5.4 \times 10^{-3} \text{ mm}$$

$$= 5.4 \times 10^{-6} \text{ m}.$$

Problem 6

From the geometry of the situation it is obvious that

$$d = \alpha R \quad (i)$$

-e α is the angle of the cone which is the onomatadia. If this angle is at the minimum given by Rayleigh's criterion:

$$\alpha = 0.61\ \lambda/r = 1.22\ \lambda/d \quad (ii)$$

Combining equations (i) and (ii) and solving for d, one gets

$$d = (1.22R\lambda)^{1/2}.$$

Substituting in $R = 1$ mm and $\lambda = 400$ nm gives

$$d = 2.2 \times 10^{-5}\text{m}.$$

Problem 7

$\lambda = 9.67 \times 10^{-4}$m

r = striking distance $\approx$ 1 m

s = accuracy of strike $\approx$ 2 cm

$\phi = s/r = 2 \times 10^{-2}$ rad.

Using the Rayleigh criterion, the separation of the pits, d, is given by by

$$d = 2.(0.61)\lambda/\alpha = 1.22\ \frac{9.67 \times 10^{-4}\text{m}}{2 \times 10^{-2}\text{ rad}} \approx 6 \times 10^{-2}\text{m}$$

$\approx$ 6 cm.

This theoretical prediction corresponds very closely to the actual observed separation of the infrared sensing organs of a pit viper.

Problem 8

The echo will return after:

$$T = d/c_s = 10\text{m}/350\ \text{m s}^{-1} = 28.6\ \text{ms}.$$

The insect detects a frequency:

$$f_i = (C_s + V_i)f_s/(C_s - V_L)$$

which is reflected to the bat and detected at the frequency:

$$f_L = (C_s + V_L)f_i/(C_s - V_i) = \frac{350 + 5}{350 - 1}\left[\frac{350 + 1}{350 - 5}\right] 50\ \text{kHz}$$

$$= 51.74\ \text{kHz}.$$