

signals dictate preferential synthesis of additional energy-converting machinery, formation of other cell components essential for rapid growth [such as ribosomes (18)] would be inhibited and, inevitably, the growth rate would be decelerated. A regulatory system performing in this fashion should be characterized as a partially compensatory control mechanism rather than as a finely tuned regulation device. It seems likely that in addition to changes in quantity, changes in composition of energy-converting membranes must occur under different nutritional conditions to permit economic use of the energy and material resources available for biosynthesis. It is hoped that polymyxin and related antibiotics will serve as sensitive reagents for defining such alterations.

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#### References and Notes

1. A. L. Tuttle and H. Gest, *Proc. Nat. Acad. Sci. U.S.A.* **45**, 1261 (1959).
  2. G. Cohen-Bazire and W. R. Sistrom, in *The Chlorophylls*, L. P. Vernon and G. R. Seeley, Eds. (Academic Press, New York, 1966), p. 313.
  3. ———, R. Y. Stanier, *J. Cell. Comp. Physiol.* **49**, 25 (1957); W. R. Sistrom, *J. Gen. Microbiol.* **28**, 607 (1962).
  4. G. A. Sojka, G. A. Din, H. Gest, *Nature* **216**, 1021 (1967).
  5. G. A. Sojka and H. Gest, *Proc. Nat. Acad. Sci. U.S.A.* **61**, 1486 (1968).
  6. G. Cohen-Bazire and R. Kunisawa, *J. Cell Biol.* **16**, 401 (1963).
  7. S. C. Holt and A. G. Marr, *J. Bacteriol.* **89**, 1421 (1965).
  8. A. Gorchein, *Proc. Roy. Soc. (London) Ser. B* **170**, 247 (1968).
  9. S. P. Gibbs, W. R. Sistrom, P. B. Worden, *J. Cell Biol.* **26**, 395 (1965).
  10. J. Schröder and G. Drews, *Arch. Mikrobiol.* **64**, 59 (1968).
  11. J. Lascelles, in *Advances in Microbial Physiology*, A. H. Rose and J. F. Wilkinson, Eds. (Academic Press, New York, 1968), vol. 2, p. 1.
  12. D. S. Steiner, J. C. Burnham, R. L. Lester, S. F. Conti, *Bacteriol. Proc.* (1969), p. 140.
  13. B. A. Newton, *Bacteriol. Rev.* **20**, 14 (1956); in *The Strategy of Chemotherapy*, S. T. Cowan and E. Rowatt, Eds. (Cambridge Univ. Press, Cambridge, 1958), p. 62.
  14. K. Wahn, G. Lutsch, T. Rockstroh, K. Zapf, *Arch. Mikrobiol.* **63**, 103 (1968); M. Koike, K. Iida, T. Matsuo, *J. Bacteriol.* **97**, 448 (1969).
  15. J. W. Newton, *Biochim. Biophys. Acta* **165**, 534 (1968).
  16. A similar effect of polymyxin on the permeability of *Pseudomonas aeruginosa* cells to the dye *N*-tolyl- $\alpha$ -naphthylamine-8-sulphonic acid has been reported by B. A. Newton [*J. Gen. Microbiol.* **10**, 491 (1954)].
  17. G. H. Warren, J. Gray, J. A. Yurchenco, *J. Bacteriol.* **74**, 788 (1957).
  18. G. A. Din and H. Gest, *ibid.* **97**, 1518 (1969).
  19. C. H. Fiske and Y. Subbarow, *J. Biol. Chem.* **66**, 375 (1925).
  20. M. Avron, *Biochim. Biophys. Acta* **40**, 257 (1960).
  21. Supported by NSF grant GB-7333X. We thank Theresa Young and Susan Ray for expert technical assistance.
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17 July 1969

3 OCTOBER 1969

## Thermal Radiation in Metabolic Chambers

Abstract. *Emissivities and ratios of surface areas of metabolic chambers and their contents have been usually ignored in studies of the metabolic rates of animals. Failure to take these factors into account can lead to errors in the interpretation of results.*

A wide variety of containers have been used to measure metabolic heat production and the rates of evaporative water loss of animals. Frequently, such chambers have had smooth metallic inner surfaces. Generally, such metallic surfaces have high infrared reflectances and low emissivities (1). The exchange of thermal radiation between the animal and the chamber walls is often not considered. If the chamber walls are highly reflective to infrared radiation, the energy reflected back to the animal from the chamber walls may have a significant effect on the energy balance of the animal (2).

The exchange of radiant energy between an animal (or plant) and a closed chamber is determined by the surface temperatures and emissivities of the organism and the container walls, their surface areas, and the percentage of each area that "views" the other (the view factor) (3, 4). An equation that describes the theoretical exchange of radiation between an object and its container may be derived in at least two ways. In an intuitive derivation one may imagine two infinite parallel planes with a finite surface between them. The infinite planes represent the container walls and the finite surface rep-

resents the organism. We here assume for simplicity that the absorptivity of the animal is perfect, that is, absorptivity is 1. Energy radiated from an animal (designated surface 1) will strike surface 2 (the infinite parallel planes) where a fraction will be absorbed and some will be reflected. The proportion of the reflected energy incident on surface 1 will be determined by the view (shape) factor from surface 2 to surface 1 ( $F_{21}$ ) (3). The rest will pass the animal and be absorbed or reflected by the opposite plane. On each pass of reflected energy, some falls on the animal. The equation describing the transfer of radiant energy from surface 1 to surface 2 is

$$E_{1 \rightarrow 2} = \alpha_2 \epsilon_1 \sigma T_1^4 A_1 + \alpha_2 [\rho_2 (\epsilon_1 \sigma T_1^4 A_1) - \rho_2 (\epsilon_1 \sigma T_1^4 A_1) F_{21}] + \alpha_2 \rho_2 [\rho_2 (\epsilon_1 A_1 \sigma T_1^4) - \rho_2 (\epsilon_1 A_1 \sigma T_1^4) F_{21}] - \alpha_2 \rho_2 [\rho_2 (\epsilon_1 A_1 \sigma T_1^4) - \rho_2 (\epsilon_1 A_1 \sigma T_1^4) F_{21}] F_{21} + \dots \quad (1)$$

or

$$E_{1 \rightarrow 2} = \alpha_2 \epsilon_1 A_1 \sigma T_1^4 [1 + \rho_2 (1 - F_{21}) + \rho_2^2 (1 - F_{21})^2 + \rho_2^3 (1 - F_{21})^3 \dots] \quad (2)$$

where  $\alpha$  is the absorptivity,  $\epsilon$  is the emissivity,  $\rho$  is the reflectivity,  $\sigma$  is the Stefan-Boltzmann constant,  $T$  is the surface temperature in  $^{\circ}\text{K}$ , and  $A$  is the surface area.

Since Eqs. 1 and 2 have the form

$$1 + x + x^2 + x^3 \dots = 1/(1 - x) \quad (3)$$

then

$$E_{12} = \frac{\alpha_2 \epsilon_1 A_1 \sigma T_1^4}{1 - \rho_2 (1 - F_{21})} \quad (4)$$

In similar fashion the radiant energy transferred from surface 2 to surface 1 is

$$E_{21} = \frac{\alpha_2 \epsilon_2 A_2 \sigma T_2^4}{1 - \rho_2 (1 - F_{21})} \quad (5)$$

Since the net energy transferred by radiation is the difference between Eqs. 4 and 5 and  $A_1 F_{12} = A_2 F_{21}$ ,  $F_{12} = 1$ ,  $\alpha = \epsilon$ , and  $\alpha + \rho = 1$  (5). Equation 6 is similar to Christiansen's equation (6).

$$Q_{12} = \frac{\epsilon_1 \epsilon_2 A_1 \sigma (T_1^4 - T_2^4)}{1 + (1/\epsilon_2 - 1)(A_1/A_2)} \quad (6)$$

where  $Q_{12}$  is the net transfer of energy from surface 1 to surface 2. A more

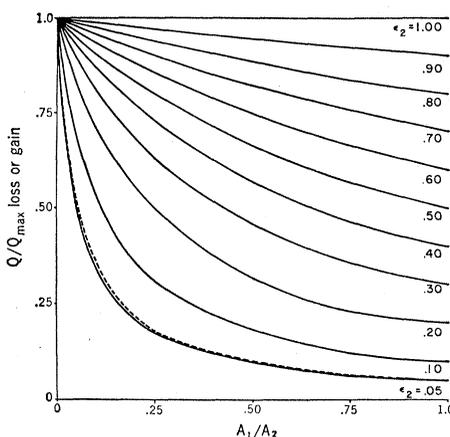


Fig. 1. Ratio of actual net radiant exchange to maximum possible net exchange as a function of area ratios and container emissivities. Maximum net exchange occurs when both surfaces have an emissivity of 1.0. All solid lines are computed on the assumption that the animal surface has an emissivity of 1.0. The dashed line is the difference in the solution at  $\epsilon_2 = 0.05$  if  $\epsilon_1 = 0.95$  instead of 1.0. The difference is even smaller at higher values of  $\epsilon_2$ .

sophisticated derivation (7, 8) yields a more general equation

$$Q_{12} = \frac{\epsilon_1 \epsilon_2 A_1 \sigma (T_1^4 - T_2^4)}{1 + (1 - \epsilon_2) (\epsilon_1 A_1 / \epsilon_2 A_2)} \quad (7)$$

which reduces to Eq. 6 when  $\epsilon_1 = 1$ .

Figure 1 shows the ratio of actual  $Q_{12}$  to maximum  $Q_{12}$  for different area ratios and different container emissivities. When a very small animal is placed in a large metabolic chamber,  $A_1/A_2$  approaches zero and  $Q$  approaches  $Q_{\max}$ . At a high wall emissivity, for example, 1.0, and a wall temperature equal to air temperature, for a given set of environmental conditions there will be a maximum energy loss from the animal by thermal radiation and a minimum energy loss by convection because the solution for surface temperature given in Eqs. 8 and 9 (shown below) is a minimum compared to the value when wall emissivity is low, for example, 0.05. Conversely, when an animal nearly fills a chamber,  $A_1/A_2$  approaches 1 and most of the energy radiated from the animal is reflected back to it at low emissivities. Under these conditions the net radiant heat loss is a minimum, and the convective heat loss and surface temperature solution are maximums. If the animal's insulation, core temperature, and evaporative water losses are assumed to be constant, the metabolic requirements for the maintenance of the same body temperature are less than when wall emissivity is 1.0. This reduced metabolic requirement is the result of the animal's intercepting a greater percentage of its own reradiated energy, thereby increasing its surface temperature and reducing the temperature difference between its surface and its core. Consequently, less heat will be conducted across the body wall. Less metabolic heat production is necessary

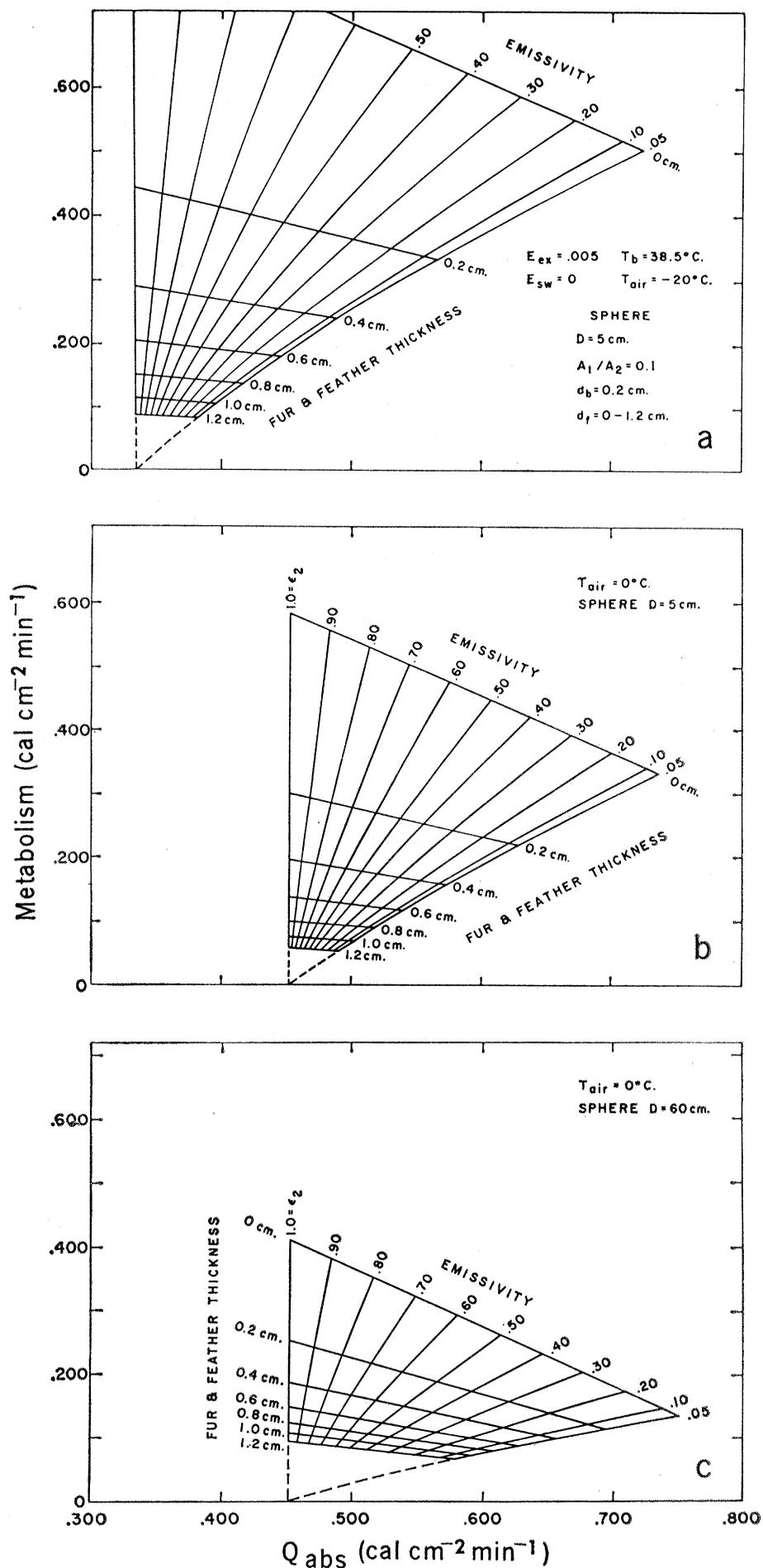


Fig. 2. Comparison of metabolic requirements at different chamber emissivities. Values used in the computations are listed in (a). Assumed wind speed is 10 cm/sec. The quantity  $Q_{abs}$  is the sum of the thermal radiation emitted and reflected from chamber walls that is absorbed by the animal. Conductivity of fur was assumed to be that of still air; this assumption is a little optimistic (11), but the thicknesses of the insulation can be considered effective rather than actual thicknesses. Surface temperatures at a given thickness of insulation are different at each emissivity but are not plotted here. There is one and only one surface temperature solution for each combination of an animal's physical and physiological properties and a specific physical environment.

to achieve the same equilibrium body temperature. Therefore, at low wall emissivities a relatively high surface temperature means that an animal may not be under nearly as great a cold stress as might be assumed from measurements of air temperature alone. Interpretations of an animal's tolerances to cold environments may lead to overestimates of an animal's capabilities. Interpretations of tolerances to warm environments can also be misleading, since at low wall emissivities the sum of emitted and reflected thermal radiation from the walls may be only slightly higher than the energy radiating from the surface of the animal.

Since physiological studies of metabolism are usually correlated to air temperature, Fig. 2 shows the changes in metabolism that might be expected at a fixed air temperature for different thicknesses of fur or feathers of model spherical animals. I determined the points on these graphs by using a computer program that simultaneously solves Eqs. 8 and 9.

$$T_r = T_b - \frac{(M - E_{ex}) A_s}{4\pi r_b r_s k_b / (r_s - r_b)} - \frac{(M - E_{ex} - E_{sw}) A_f}{4\pi r_f r_s k_f / (r_f - r_s)} \quad (8)$$

Equation 8 was derived from Eq. 7, Porter and Gate's figure 4 (2), and Birkebak's equation (4) for heat conducted to a sphere's surface. Equation 8 describes the steady-state heat transfer between the core of a sphere and its surface. Equation 9 describes the steady-state heat transfer between the surface of the sphere and its environment.

$$M = Q_{12} + C + E_{ex} + E_{sw} \quad (9)$$

In these equations  $M$  is the metabolic heat production,  $E_{ex}$  is the energy lost by evaporation during breathing (in calories per square centimeter per minute),  $E_{sw}$  is the energy lost by water evaporating from the skin,  $T_r$  is the surface temperature,  $T_b$  is the body (core) temperature,  $A_s$  is the skin area,  $r_s$  is the radius of the sphere to the skin,  $r_b$  is the radius out to the point in the body wall where temperature begins to drop from the core temperature (2),  $k_b$  is the conductivity of flesh (9),  $A_f$  is the surface area of fur or feathers,  $r_f$  is the radius to the effective radiating temperature of the fur (2),  $k_f$  is the fur conductivity, and  $C$  is the convection from a sphere at the appropriate Reynolds number (3). Conductive

heat loss is assumed to be negligible and has not been included.

The assumptions used in Fig. 2, a and b, are that the animal has curled into a ball whose outside diameter is 5 cm (about the body diameter of a cardinal). The only difference in the values used to compute the points in Fig. 2, a and b, is the air temperature. The vertical line,  $\epsilon_2 = 1.0$ , indicates the energy absorbed from black surfaces at  $-20^\circ\text{C}$  and  $0^\circ\text{C}$ , respectively. A comparison of Fig. 2a with Fig. 2b indicates that over the full range of emissivities the change in metabolic requirements at a given thickness of insulation is dependent on the magnitude of the difference between the core and the air temperature.

Figure 2c is an extreme, hypothetical example which shows how a large animal curled into a spherical shape could be expected to respond to changes in wall emissivity. For identical environments (Fig. 2, b and c) metabolic requirements are less for a 60-cm spherical shape than for a 5-cm spherical shape because a larger object has a thicker boundary layer (2, 10) that insulates its surface more effectively from air temperature. Since a larger object with little fur is not cooled as much by convection, less metabolic heat is required, for example, at  $\epsilon_2 = 1.0$ , to maintain a body temperature of  $38.5^\circ\text{C}$  at an air temperature of  $0^\circ\text{C}$ .

Thus, in order to keep  $Q/Q_{\max}$  (Fig. 1) as close to 1 as possible and thereby to minimize complications involving view factors and reflected ther-

mal radiation in metabolic chambers, wall emissivity should approach 1. Alternatively, if material of lower emissivity is essential for chamber construction, the container should be as large as possible relative to the organism's size so as to keep the ratio of surface areas,  $A_1/A_2$ , small. If neither course is possible, area ratios and wall emissivities must be determined to accurately establish an animal or plant's absorbed thermal radiation.

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#### References and Notes

1. G. G. Gubareff, J. E. Janssen, R. H. Torborg, *Thermal Radiation Properties Survey* (Honeywell Research Center, Minneapolis, 1960).
2. W. P. Porter and D. M. Gates, *Ecol. Monogr.*, in press.
3. F. Kreith, *Principles of Heat Transfer* (International Textbook, Scranton, Pa., 1965).
4. R. C. Birkebak, *Int. Rev. Gen. Exp. Zool.* **2**, 269 (1966).
5. W. P. Porter and K. S. Norris, *Science* **163**, 482 (1969).
6. A. J. Ede, *An Introduction to Heat Transfer* (Pergamon, New York, 1967).
7. W. A. Beckman, in *Proceedings of the 1968 Aviation and Space Conference* (American Soc. of Mechanical Engineers, New York, 1968).
8. W. P. Porter and J. W. Mitchell, in preparation.
9. M. Lipkin and J. D. Hardy, *J. Appl. Physiol.* **7**, 212 (1954).
10. D. M. Gates, *Energy Exchange in the Biosphere* (Harper & Row, New York, 1962).
11. H. T. Hammel, *Amer. J. Physiol.* **182**, 369 (1955).
12. I thank Dr. J. W. Mitchell of the Mechanical Engineering Department for deriving Eq. 7. Drs. J. W. Mitchell and G. Myers reviewed this manuscript and made helpful criticisms and suggestions. I also thank Miss C. Hughes for illustrations, D. Chandler for photography, and Mrs. A. Chambers for typing. Supported in part by the Wisconsin Alumni Research Foundation through the University Research Committee.

26 May 1969; revised 22 July 1969

## Virus of the 1918 Influenza Pandemic Era: New Evidence about Its Antigenic Character

**Abstract.** *In serums of unusually isolated Pacific islanders whose only exposure to influenza occurred during the era of the 1918 pandemic the residual neutralizing antibody was greatest to the PR/8 and BH strains of human type A influenza virus, significantly lower to swine influenza virus, and absent to equine or later human type A virus strains. The pandemic virus was thus antigenically closer to human type A strains isolated during the middle 1930's than to other known influenza virus types.*

During the course of our studies of the immune response to influenza vaccines in isolated Pacific island populations (1), we discovered in 1964 that the population of one particularly inaccessible western Caroline island, Fais, had not experienced type A influenza for several decades. In a total population of over 200, not a single individual

born after 1924 and who had never been off the island had neutralizing antibody to any of several strains of virus spanning the subgroups of influenza virus type A. Antibody to the early subtype A strains, however, was evenly spread throughout the older age groups in approximately half of the 80 people born before 1924.