

## COOLING RATE AND SIZE OF BIRDS' EGGS—A NATURAL ISOMORPHIC BODY

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**Abstract**—The resistance to heat transfer of birds' eggs scales not to the  $-2/3$  power of egg mass, as would be expected for an isomorphic object, but to the  $-0.60$  power. This unexpected exponent apparently is the result of the composite resistance to heat exchange by both radiation and convection.

### INTRODUCTION

The transfer of heat from the surface of an organism is usually thought to depend on surface area. The surface area of an isomorphic body (one which does not change shape with respect to size) varies exponentially with the  $2/3$  power of volume. It often has been suggested that the conductance to heat transfer of animals therefore should scale with body size with the  $2/3$  power of mass (Schmidt-Nielsen, 1983). It is noteworthy, then, that the exponent relating conductance of animals to their mass is not  $2/3$  but actually is closer to 0.5 (Bartholomew, 1977). Any departure from a scaling exponent of  $2/3$  usually is taken as evidence that animals are not isomorphic, with either density, surface area or some other property of the animal scaling in some unusual way with mass (Bartholomew, 1977; Heusner, 1982a, b).

Heat exchange depends not only on properties of the animals themselves, so-called intrinsic properties such as surface area, but also on factors external to the organism, so-called extrinsic properties such as the thickness of boundary layers of air (Kleiber, 1972; Tracy, 1972). Because of this, the heat exchange even from isomorphic bodies may not scale exponentially with size, but in more subtle ways. In this paper, I develop this argument explicitly. I first show that there is no *a priori* reason to expect heat exchange to always follow an exponential relationship with size. I then show that forcing predicted values for heat exchange from spheres into an exponential model results in an apparent scaling exponent somewhat less than  $2/3$ , under conditions of free convection. Finally, I support my theoretical arguments with data on the variation with size of the cooling rates of a natural isomorphic body, birds' eggs.

### HEAT TRANSFER FROM SPHERES

A sphere is the classic example of an isomorphic body. In the predictions developed below, I assume a sphere that exchanges heat with air by free convection and with the walls of a chamber by radiation. The temperature of the chamber walls is assumed to be equivalent in temperature to the air temperature, and evaporation and conduction are assumed to be negligible avenues of heat exchange. A resistance

to heat transfer can be assigned to both convection ( $R_c$ ;  $\text{K W}^{-1}$ ) and radiation ( $R_r$ ). Because convection and radiation heat exchanges occur simultaneously, the total resistance to heat transfer ( $R_t$ ) is comprised of the parallel resistances for both convection and radiation:

$$1/R_t = 1/R_r + 1/R_c; \quad (1)$$

resistance is the inverse of the more commonly used term of conductance ( $\text{W K}^{-1}$ ).

The calculation of the resistances to heat transfer from spheres is well worked out (Thomas, 1980). For radiation resistance:

$$R_r = 1/\epsilon\sigma A(T_s + T_e)(T_s^2 + T_e^2), \quad (2)$$

where  $\epsilon$  = emissivity (assumed to be 0.95),  $\sigma$  = Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ),  $T_s$ ,  $T_e$  = temperatures of the surface (assumed to be 308.15 K for this example) and environment (assumed to be 298.15 K for this example), respectively, and  $A$  = surface area ( $\text{m}^2$ ). In this equation, the only term which depends upon size is  $A$ . If one calculates values of  $R_r$  for spheres of 0.001–2 m radius, radiation resistance scales in the expected way with volume:

$$R_r = 0.034 V^{-0.67}. \quad (3)$$

For convection resistance:

$$R_c = 1/h_c A, \quad (4)$$

where  $h_c$  = convection coefficient ( $\text{W K}^{-1} \text{ m}^{-2}$ ). Here, two terms depend upon size, area and the convection coefficient. The convection coefficient is calculated from a dimensionless number, the Nusselt number (Nu):

$$\text{Nu} = h_c D/k_a, \quad (5)$$

where  $D$  = diameter of the sphere (m) and  $k_a$  = thermal conductivity of air ( $\text{W m}^{-1} \text{ K}^{-1}$ ). The Nusselt number itself is calculated from two other dimensionless numbers, the Grashof number (Gr) and the Prandtl number (Pr). For free convection:

$$\text{Nu} = 2 + 0.43 (\text{Gr Pr})^{0.25}; \quad (6)$$

the Prandtl number is

$$\text{Pr} = \mu c_p/k_a, \quad (7)$$

where  $\mu$  = dynamic viscosity of air ( $\text{kg m}^{-1} \text{ s}^{-1}$ ) and  $c_p$  = specific heat of air ( $\text{J kg}^{-1} \text{ K}^{-1}$ ). The Prandtl number does not depend upon size and has a value

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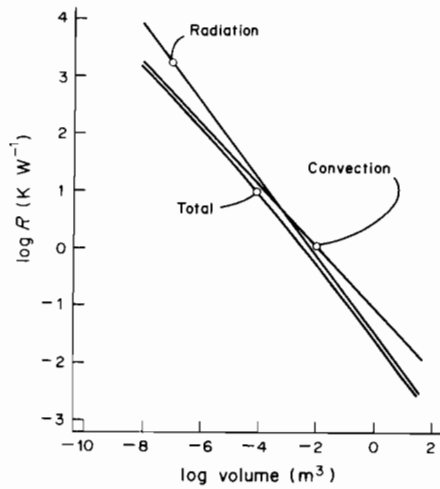


Fig. 1. Predicted values for resistances to heat transfer ( $\text{K W}^{-1}$ ) from the surface of spheres.

of about 0.71. The Grashof number is

$$\text{Gr} = g\beta D^3(T_s - T_t)/\nu^2, \quad (8)$$

where  $g$  = gravitational acceleration ( $\text{m s}^{-2}$ ),  $\beta$  = coefficient of thermal expansion ( $\text{K}^{-1}$ ) and  $\nu$  = kinematic viscosity of air ( $\text{m}^2 \text{s}^{-1}$ ). The Grashof number clearly depends upon size of the sphere. The values of convection resistance may be calculated for spheres using equations 5, 6, 7 and 8 along with tabulated values for the properties of air (Tracy *et al.*, 1980). Again, one can calculate  $R_c$  for spheres from 0.001 to 2 m radius, and:

$$R_c = 0.097 V^{-0.54}. \quad (9)$$

When radiation and convection resistances combine, the resulting total resistance does not scale exponentially with volume of the sphere. The plot of the logarithm of total resistance vs logarithm of the volume is not linear, as would be expected if the two values were exponentially related (Fig. 1). Rather, the double-log plot of  $R_t$  vs  $V$  is hyperbolic, approaching convection resistance asymptotically at small sizes, and approaching radiation resistance asymptotically at large sizes (Fig. 1). If one nevertheless fits a linear model to the predicted values of  $\log R_t$ , the relationship is

$$R_t = 0.027 V^{-0.60}, \quad r^2 = 0.998. \quad (10)$$

Confidence limits about this exponent at  $P = 0.05$  are  $\pm 0.0184$ .

## MATERIALS AND METHODS

### Cooling rates of birds' eggs

Blown eggshells for 32 species of birds (34 eggs total) were obtained from museum collections in the Department of Zoology, Duke University (Table 1). The blown eggshells were filled with scrambled, uncooked hens' egg. A thermocouple was fixed to the egg with beeswax, so that the junction (copper-constantan, 36 Ga) was approximately in the centre of the egg. The hole in the egg was sealed with a thin

Table 1. Characteristics of eggs used for cooling-curve analyses

Species	Length (mm)	Breadth (mm)	Mass (g)	Time constant (s)
Bluegray gnatcatcher	15.0	11.7	1.12	479
Chimney swallow	21.8	13.3	1.92	615
Phoebe	18.8	15.0	2.21	674
Bluegray gnatcatcher	21.9	15.5	2.88	742
Bluebird	21.3	16.3	3.17	772
Kingbird	18.8	15.0	3.40	727
Catbird	23.8	17.4	3.80	860
Bluejay	24.0	18.4	4.10	905
Robin	28.5	20.1	5.96	1039
Flicker	26.5	21.2	6.44	1128
Meadowlark	29.0	21.0	6.64	1071
Brown thrasher	29.1	20.9	6.73	1101
Whippoorwill	29.3	21.4	7.15	1132
Kestrel	27.3	22.5	7.29	1083
Nighthawk	30.9	22.4	8.32	1202
Bobwhite	31.6	24.2	9.19	1221
Kildeer	38.1	25.8	11.80	1346
Screech owl	33.7	29.3	18.33	1530
Crow	41.5	30.4	19.34	1738
Crow	41.3	29.2	20.19	1553
Glossy ibis	50.2	38.8	39.98	2193
Barred owl	48.4	41.3	40.16	2350
Red-shouldered hawk	52.1	42.2	46.44	2376
Night heron	55.5	40.2	48.16	2619
Oystercatcher	59.2	41.1	48.95	2368
Canvasback	65.5	44.2	65.50	2859
Osprey	67.8	44.8	70.47	2577
White-fronted goose	69.6	48.5	85.01	3226
Black brant	71.9	48.4	86.57	3236
Turkey vulture	71.2	49.8	96.00	3094
Wild turkey	73.7	50.8	100.98	3381
Black vulture	70.7	51.0	106.02	3603
Emperor penguin	132.1	96.1	682.72	5446
Ostrich	155.9	130.3	1516.16	8866

plug of tissue paper and beeswax, to prevent the contents from leaking out during the experiment.

The filled eggs were warmed to  $37^\circ\text{C}$  in an incubating oven. When the egg temperature had equilibrated, the egg was transferred to a platform in a large environmental chamber that was kept at  $25^\circ\text{C}$ . The surface on which the egg rested was a mesh of fine plastic wire (window screen). While the egg cooled, the circulating fans and regulating machinery of the environmental chamber were disabled, to ensure conditions of free convection. Egg temperature was automatically recorded onto magnetic tape. Time constants for cooling,  $\tau$  (s) were calculated from the data using the method of Bakken (1976). Total resistance to heat transfer was calculated from the time constant:

$$\tau = R_t C \quad (11)$$

$$R_t = \tau/C, \quad (11a)$$

where  $C$  = capacitance of the egg. Capacitance is calculated by

$$C = Mc_e, \quad (12)$$

where  $M$  = mass of egg (kg) and  $c_e$  = specific heat of egg ( $3313 \text{ J kg}^{-1} \text{ K}^{-1}$ ; Romanoff and Romanoff, 1949).

### Shape of eggs

Variation in the eccentricity of an egg can introduce significant errors in the estimated surface area (Hoyt, 1976). Eccentricity ( $e$ ) of the eggs were calculated:

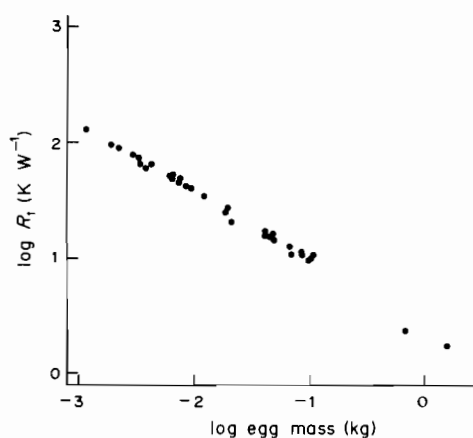


Fig. 2. The relationship between log of the total resistance to heat transfer ( $\text{K W}^{-1}$ ) and log of the mass of the filled egg (kg).

$$e = [(L^2 - B^2)/L]^{1/2}, \quad (13)$$

where  $L$  = length and  $B$  = breadth. Length, breadth and mass of each egg was measured immediately after cooling. Volume of the egg was estimated using the data of Hoyt (1976) and data on egg lengths and breadths reported in Harrison (1978).

#### RESULTS

Time constants for the filled eggs are reported in Table 1. The relationship between the time constant (s) and egg mass (kg) is

$$\begin{aligned} \tau &= 7998 M^{0.402}, \\ r^2 &= 0.990. \end{aligned} \quad (14)$$

Resistance to heat transfer scales with egg mass (Fig. 2):

$$\begin{aligned} R_t &= 2.42 M^{-0.598}, \\ r^2 &= 0.995. \end{aligned} \quad (15)$$

Eccentricity does not contribute significantly to variation in the time constant ( $P = 0.508$ ) and does not vary significantly with egg mass ( $P = 0.899$ ). Estimated volumes of the eggs were calculated by

$$\ln V = -0.671 + 0.991 \ln (LB^2), \quad (16)$$

where  $V$  = volume ( $\text{mm}^3$ ). The relationship between the estimated volume ( $\text{m}^3$ ) and egg mass (kg) is

$$\begin{aligned} M &= 1174 V^{1.002}, \\ r^2 &= 0.997. \end{aligned} \quad (17)$$

#### DISCUSSION

The theoretical discussion of heat transfer from spheres and the data on cooling rates of eggs reported here underscore two major points about heat transfer from organisms: (1) transfers of heat do not necessarily scale with the  $2/3$  power of mass, even in isomorphic bodies; (2) transfers of heat do not necessarily scale exponentially with body mass, but may scale in more complex ways.

The first conclusion is well-supported by theory. However, the accompanying empirical support may

be weakened if (a) the eggs used in this study were not isomorphic, or (b) something other than convection or radiation was a significant avenue of heat loss.

Isomorphy can only be assumed if density does not vary with size and if area truly scales with the  $2/3$  power of volume. A systematic error in time constant arising from changes in density with size may be ruled out in this case for two reasons. The filling of the egg was always the same material, i.e. scrambled uncooked hen's egg. Also, mass scales with the estimated volume of the egg to the power of unity [equation (17)]—by definition, a constant density.

Likewise, a systematic deviation of surface area from the  $2/3$  power of volume also can be ruled out. Previous studies of birds' eggs show clearly that surface area scales precisely to the  $2/3$  power of volume (Paganelli *et al.*, 1974). However, changes in eccentricity can introduce substantial variation in the surface area of an egg of a given volume (Hoyt, 1976). If the sample of eggs used in this study contained a systematic variation in shape with respect to mass, the eggs could not be considered isomorphic. This does not seem to be a problem in this experiment: eccentricity does not vary significantly with mass, and eccentricity does not contribute significantly to the variance in the time constant.

With respect to unconsidered avenues of heat loss, the only likely candidates are evaporation of water across the eggshell and conduction through the platform on which the egg rested. Neither are likely to contribute significantly to total resistance in this case. Using typical values for water vapour conductance through eggshells (Ar *et al.*, 1974), it is readily shown that in the most extreme case, resistance to evaporation heat loss is more than three orders of magnitude greater than the total resistance measured. Heat loss through conduction to the platform is more problematical. Conduction will be important only if (a) a large portion of the egg surface is in contact with the substrate and (b) conduction resistance of the substrate is small with respect to the total resistance of the egg. The substrate in this experiment was a sheet of plastic mesh used for window screen. Thus, the total area of contact between the egg and platform is small. Also, thin wires tend to have a high conduction resistance, and this is expected for the plastic mesh.

The results reported here suggest that the common assumption that heat transfer scales exponentially with mass may not always be a good one. In some circumstances, such as when either convection or radiation dominates heat transfer almost completely, it may be safe to proceed on the assumption that heat transfer is an exponential function of size. However, with just two modes of simultaneous heat transfer, we see that logarithm of the resistance does not vary linearly with the logarithm of mass, but hyperbolically. The scaling is likely to be even more complex if more modes of heat transfer, such as evaporation, become important. The fact that a linear model has good predictive value, and can be fitted to the predicted values with a closeness that is impressive by usual criteria [explained variance greater than 99%; equation (10)] does not lessen the fact that the *a priori* assumption of linearity may obscure important mechanisms of heat transfer.

One other general conclusion about size and thermal energetics is perhaps worth mentioning. Caution may be advisable in making inferences about properties of animals from transfers of heat. As mentioned in the Introduction, any departure of the scaling of heat exchange (as measured by conductance) from the  $2/3$  power of mass often is taken as presumptive evidence that animals are not isomorphic (Bartholomew, 1977; Heusner, 1982a, b). By the same token, conformity of conductance to the  $2/3$  power of mass is sometimes taken as presumptive evidence that isomorphy applies (Heusner, 1982a, b). Inferences such as these proceed from the implicit assumption that transfers of heat depend solely on properties of the animals themselves. It is noteworthy that the apparent exponent relating resistance to heat transfer with mass of egg apparently depends in part upon a property of the egg (the surface area) and in part on a combined property of the egg and the fluid medium for heat exchange (the convection coefficient). Thus, the scaling of heat exchange with mass depends not only on measurable properties of organisms, but also on the environmental context in which heat transfer occurs.

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