

WHY ARE SMALL HOMEOTHERMS BORN NAKED? INSULATION AND THE CRITICAL RADIUS CONCEPT

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Abstract—1. For cylinders or spheres smaller than a critical size, a layer of insulation may increase, rather than decrease, the rate of heat exchange.

2. It has been suggested that the critical size for animals insulated with fur or feathers is about 4–7 g body mass, and therefore may explain why many small mammals and birds are born naked. We suggest that this is unlikely.

3. We found that downy feathers on hatchlings as small as 1.6 g body mass retard rates of heat loss. Also, hatchling birds smaller than 4–7 g are not always, or even often, born naked.

4. If a critical size exists at all, it is likely to occur at body masses of 0.6 g or smaller.

Key Word Index—Altriciality; body size; critical radius; heat exchange; insulation.

INTRODUCTION

The critical radius effect is an interesting phenomenon of heat transfer in insulated circular solids. Briefly, the critical radius is a size limit. Insulating a cylinder or sphere larger than the critical radius has the expected effect of retarding heat loss. If a cylinder or sphere is smaller than the critical radius, adding insulation will actually increase heat loss (McAdams, 1954; Thomas, 1980).

In 1977, Balmer and Strobusch advanced the remarkable hypothesis that the naked condition of many newborn mammals and birds might be explained by the critical radius effect. These authors suggested that for neonates smaller than the critical size, a layer of fur or feathers could only increase heat loss and therefore would be disadvantageous energetically. They also suggested that the critical size for newborn homeotherms was as large as 4–7 g, depending on the animal's shape.

The argument of Balmer and Strobusch (1977) rested on two foundations. The first was the application of the theory of the critical radius to the problem of insulation in newborn homeotherms, combined with an extensive discussion of the theory itself. The other was the claim that many homeotherms that are born naked indeed are smaller than 4–7 g at birth, while homeotherms born with fur or feathers tend to be larger. Absent from the paper was experimental verification of their prediction.

Our paper examines these claims in some detail. We begin with a brief discussion of the physical basis for the critical radius effect. We then test the prediction that the critical size should occur at a body mass of 4–7 g. We first show that downy feathers on hatchlings much smaller than 4 g retard heat loss, and that the critical size may be substantially smaller than 1 g body mass. We then show that the presence or absence of insulation on hatchlings of the North

American birds in no way can be explained by the critical radius effect. We infer that the critical radius effect is not a good explanation for why many small homeotherms are born naked.

THE CRITICAL RADIUS CONCEPT

The concept of the critical radius has been considered extensively in other contexts, notably in physics and engineering heat transfer (McAdams, 1954; Thomas, 1980), but also by some biologists (Gunn, 1942; Strunk, 1971; Bakken and Gates, 1974). The following is a highly simplified abstract of the relevant physical principles.

Heat loss from a cylinder

Consider first an uninsulated cylinder [shown schematically in cross section in Fig. 1(a)] of length L (m), and outer radius of r_{skin} (m). The cylinder has an inner core of radius r_i that is at a uniform temperature T_b (K). The environmental temperature is T_a . The thermal conductivity of the shell is k_{skin} ($\text{W m}^{-1} \text{K}^{-1}$). It is readily shown that the resistance to conduction radially through the skin (R_{skin} ; K W^{-1}) is

$$R_{\text{skin}} = \ln(r_{\text{skin}}/r_i)/2\pi L k_{\text{skin}}. \quad (1)$$

In steady state, the heat conducted through the skin must equal the net heat loss from the surface to the surroundings. This heat loss occurs via at least two simultaneous mechanisms.

First, heat will be removed from the skin surface by convection. If the convective heat loss from the surface is q_c (W), then we may define a convective heat transfer coefficient (h_c ; $\text{W m}^{-2} \text{K}^{-1}$) such that

$$q_c = h_c 2\pi L r_{\text{skin}} (T_{\text{skin}} - T_a) \quad (2)$$

where T_{skin} is the temperature of the skin surface. The transfer coefficient includes the contributions of free convection, and under appropriate environmental circumstances, forced convection.

The second mechanism cooling the cylinder is the radiation from its surface. The amount of net radi-

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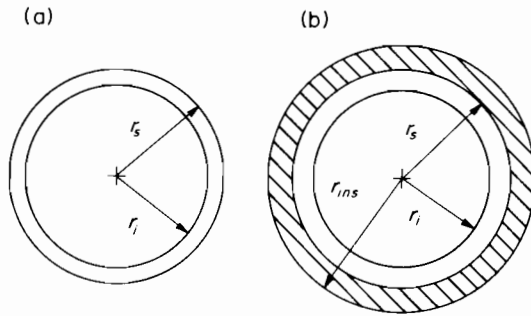


Fig. 1. Core and shell model for cylindrical objects. (a) A "naked" cylinder with the outer shell comprised of skin. (b) An insulated cylinder, with the outer shell comprised of fur or feathers and a middle shell comprised of skin.

ation between a surface and its surroundings depends upon their absolute temperatures as determined by the Stefan-Boltzmann law, the respective emissivities of the surface and the surroundings, and shape factor. For relatively small differences in temperature between the object and the surroundings ($< 10\text{ K}$; Gates, 1980), the net exchange of heat by radiation is approximately proportional to the temperature difference between the two. We may therefore define a radiant heat transfer coefficient (h_r) analogous to the convective heat transfer coefficient [equation (2)].

The total resistance to heat loss from the skin surface ($R_{\text{ext,skin}}$) is then given by

$$R_{\text{ext,skin}} = 1/[2\pi L r_{\text{skin}} (h_c + h_r)_{\text{skin}}]. \quad (3)$$

The heat loss from inner core to surroundings (q) is given by

$$q = (T_b - T_a)/R_{\text{tot}} \quad (4)$$

where

$$R_{\text{tot}} = R_{\text{skin}} + R_{\text{ext,skin}}. \quad (5)$$

We may now consider the case of a cylinder covered with a layer of insulation of thermal conductivity k_{ins} and outer radius r_{ins} as shown in Fig. 1(b). Again, it is readily shown that the conduction resistance within the insulating layer (R_{ins}) is

$$R_{\text{ins}} = \ln(r_{\text{ins}}/r_{\text{skin}})/2\pi L k_{\text{ins}}. \quad (6)$$

Similarly, heat loss from the surface of the insulation will result from both convection and radiation, and it is again reasonable to define an external resistance to heat transfer

$$R_{\text{ext,ins}} = 1/[2\pi L r_{\text{ins}} (h_c + h_r)_{\text{ins}}]. \quad (7)$$

The total resistance to heat transfer of the insulated cylinder (R_{tot}) is given by

$$R_{\text{tot}} = R_{\text{skin}} + R_{\text{ins}} + R_{\text{ext,ins}}. \quad (8)$$

Critical radius

The factors determining the existence of a critical radius can be seen if we consider first the cylinder covered only with skin. Heat loss from the inner core will increase if the total transfer resistance (R_{tot}) decreases for any reason [equation (4)]. Inspection of the two contributing terms [equation (5)] shows that the conduction resistance term increases as a function of the radius of the outer skin surface [equation (1)],

but that the external resistance decreases with increasing radius [equation (3)]. By differentiation it is possible to show that as the external radius (r_{skin}) is increased there may be a local minimum in R_{tot} , indicating a maximum in the rate of heat loss. The critical radius ($r_{\text{crit,skin}}$) at which this will happen is given by

$$r_{\text{crit,skin}} = k_{\text{skin}}/(h_c + h_r)_{\text{skin}}. \quad (9)$$

The critical radius occurs at a value determined by the ratio of the thermal conductivity through the surface layer to the total surface heat transfer coefficient—it is essentially independent of the internal radius r_i .

As a result, if the internal radius and external radius of the skin are both less than the critical value, increasing skin thickness by increasing the external radius will initially increase heat loss (Fig. 2). However, if the external radius is greater than the critical value, then increasing it further by increasing skin thickness will decrease heat loss as normally expected. It is interesting to realize that if the external radius (r_{skin}) is held constant, but skin thickness is increased by reducing r_i , then heat loss is always reduced no matter whether r_{skin} is above or below the critical value.

For the cylinder with an insulated layer covering the skin, the total resistance depends upon the additional conduction resistance through the insulation as well as the altered external resistance [equation (8)]. However, a critical radius still exists for the insulated cylinder ($r_{\text{crit,ins}}$), and is

$$r_{\text{crit,ins}} = k_{\text{ins}}/(h_c + h_r)_{\text{ins}}. \quad (10)$$

This value is less than the critical radius for skin [equation (9)]—approximately an order of magnitude less (Fig. 2), since the thermal conductivity of skin (approximately $0.4\text{ W m}^{-1}\text{ K}^{-1}$) is about an order of magnitude larger than for fur or feathers ($0.04\text{ W m}^{-1}\text{ K}^{-1}$; Schmidt-Nielsen, 1983; Walsberg *et al.*, 1978).

Two other features of the critical radius theory are worth mention. First, the value of the critical radius depends not only on the properties of the insulating layer, but also on external factors for heat exchange. While a higher thermal conductivity in the insulating layer increases the critical radius, a larger external heat transfer coefficient will push the critical radius to smaller and smaller sizes [equations (9) and (10)]. Second, while the discussion thus far has focussed on the heat exchange of cylinders, the theory is applicable to any circular solid. For example, a critical radius exists not only for cylinders, but also for spheres. The only difference is a shape factor—for a cylinder, the shape factor is unity, so that the critical radius is given by the simple ratio of the insulation's conductivity and its external heat transfer coefficient. For a sphere, the shape factor is two, and the critical radius is twice this ratio.

WHAT IS THE CRITICAL SIZE FOR AN INSULATED ANIMAL?

From the above discussion, it is obvious that there is no single critical radius for furred or feathered animals. It is reasonable, however, to predict a critical size under very limited environmental condi-

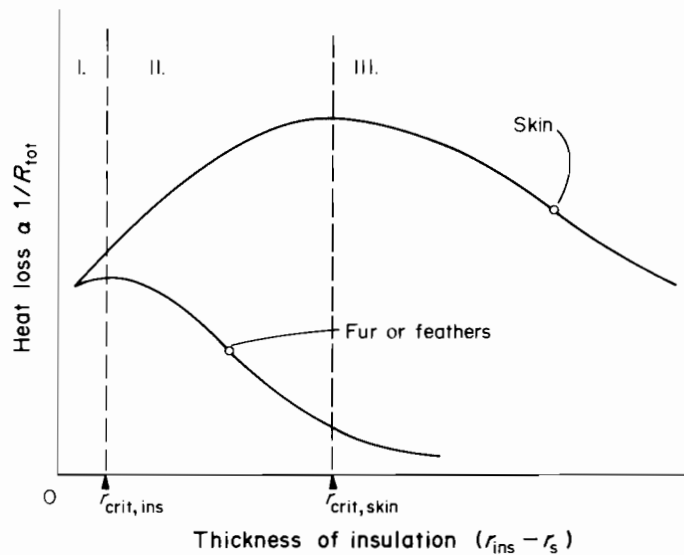


Fig. 2. Schematic depiction of the critical radii and rates of heat loss ($\propto 1/R_{tot}$) for a cylinder of size r_{skin} , smaller than both the critical radii for skin ($r_{crit,skin}$) and insulation ($r_{crit,ins}$) for varying thicknesses of the insulation layer ($r_{ins} - r_{skin}$). The upper curve represents heat loss from increasing the outer radius with greater thickness of skin. The lower curve represents heat loss from increasing the outer radius by adding layers of insulation such as fur or feathers. The figure is divided into three zones. Zone I: insulation thickness is less than the critical radius for insulation. Zone II: insulation thickness is between the critical radii for both skin and insulation. Zone III: insulation thickness is greater than the critical radius for skin.

tions. Balmer and Strobusch (1977) assumed that a neonatal mammal or bird in an enclosed nest likely would experience heat losses dominated by free convection from the body surface. Under these restricted conditions, the critical size for a cylindrical neonate should be about 4 g, and about 7 g for a spherical neonate. This prediction is readily testable. If it is true, then removing the insulating layer from an animal smaller than 4–7 g should increase its total resistance to heat loss.

We tested this hypothesis on very small bird hatchlings that have full coats of down. Total resistance to heat loss (R_{tot}) was estimated both for hatchlings with a full coat of down and after the downy coat had been removed. Experiments with living hatchlings proved unworkable, owing to their variable production of metabolic heat, and so we used dead hatchlings.

Materials and methods

We used the precocial hatchlings of two species of birds: 10 individuals of the bobwhite quail (*Colinus virginianus*) ranging in body mass from 4.30 to 9.82 g, and 9 individuals of the button quail (*Excalfactoria chinensis*), ranging in body mass from 1.60 to 3.48 g. A copper–constantan thermocouple made from wire 0.127 mm diameter was inserted into the cloaca of the feathered hatchling, and secured with a suture clip in the uropygium. The carcass was warmed to 37°C in an incubating oven. When the temperature of the carcass had equilibrated, the hatchling was transferred to an environmental chamber (1.6 m × 2.4 m × 1.9 m). To duplicate as closely as possible the conditions of free convection assumed by Balmer and Strobusch (1977) in their predictions, the regulating machinery and fans of the chamber were disabled to reduce fluctuations in temperature and air currents. The carcass rested on a screen of fine mesh

plastic, inside a cage (50 cm × 50 cm × 50 cm) of double-layered cheesecloth to further reduce stray air currents around the hatchling. The hatchling was allowed to cool, and its temperature was recorded on magnetic tape for subsequent computer analysis.

The hatchling was then removed from the chamber and its down removed using a commercial depilatory agent (Neet; Whitehall Laboratories), after which the skin was washed and gently dried. The carcass was reheated to 37°C and the cooling procedure was repeated.

Time constants, τ (s) were calculated from the cooling curves, using the method described by Bakken (1976). Resistances to heat exchange for the feathered hatchlings ($R_{tot,f}$; $K W^{-1}$) and defeathered hatchlings ($R_{tot,d}$) were calculated from the time constants by

$$R_{tot} = \tau / cM \quad (11)$$

where c = specific heat of the hatchling ($3.35 J g^{-1} K^{-1}$) and M = mass of hatchling (g).

Apart from the obvious precautions of ensuring the hatchling's skin was dry, and discarding the data from any hatchling whose skin was damaged by handling, or whose equilibrium temperature was anomalously low, we did not correct for a possible difference in evaporative heat loss between the feathered and defeathered hatchlings. In any event, evaporation is unlikely to be different between the two groups. For "dry-skinned" animals like bird hatchlings, the limiting resistance to water vapor diffusion, and hence latent evaporative heat loss, is the skin, not the pelage (Campbell, 1977). Removal of the pelage should not therefore affect latent heat loss. Also, for latent heat loss to contribute significantly to the total exchanges of heat, its resistance should be no more than one order of magnitude larger than the re-

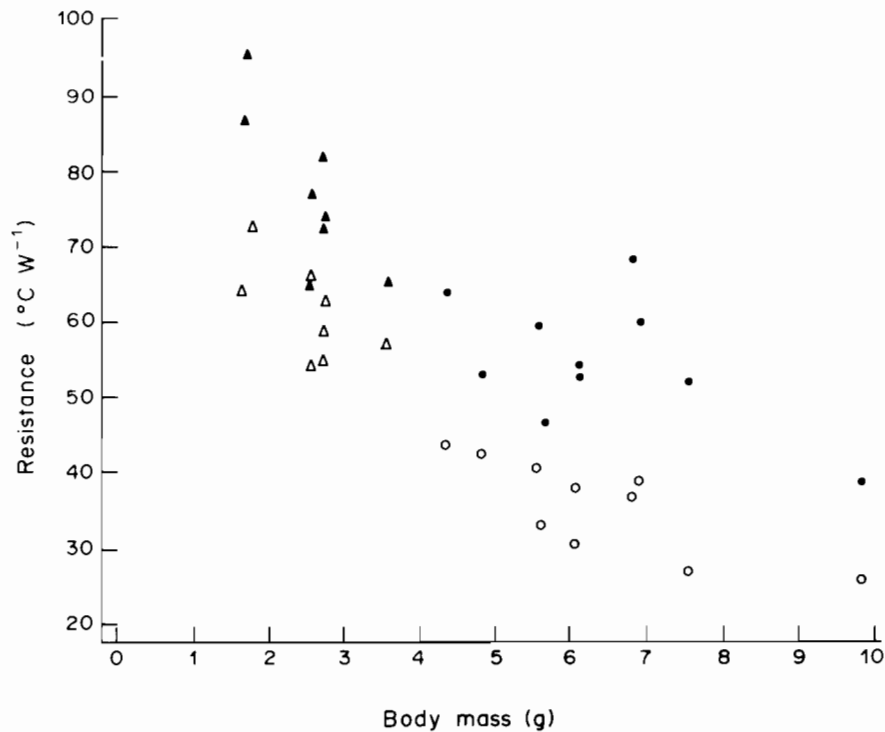


Fig. 3. The relationship between resistance to heat exchange (R_{tot} , K W^{-1}) and body mass for dead hatchlings of bobwhite and button quail. Circles are for data from bobwhite, triangles are for data from button quail. Solid symbols are for data from feathered hatchlings, open symbols are for data from defeathered hatchlings.

sistance for any other potential source of heat exchange, in this experiment, convection. The resistance to water vapor diffusion in skin of *Excalfactoria* is about 20 s m^{-1} (Campbell, 1977). We know of no comparable data for bobwhite skin, but we assume its resistance is similar to skin of button quail. A "worst case" estimate (a hatchling in dry air at the highest temperature during the transient) shows that the resistance to latent heat loss is very roughly $> 1400 \text{ K W}^{-1}$, and in our experiment was likely larger. This is at least one to two orders of magnitude larger than the resistance expected for convection heat loss (see results). We conclude therefore that evaporation is not a significant source of heat loss in this experiment, and need not be corrected for.

Results

Average resistance to heat transfer for all feathered hatchlings is 64.5 K W^{-1} . For all defeathered hatchlings, average resistance to heat transfer is 46.3 K W^{-1} . The resistances to heat loss for both feathered and defeathered hatchlings were strongly dependent upon mass (Fig. 3). For feathered hatchlings

$$R_{\text{tot},f} = 106 M^{-0.373 \pm 0.111} \quad (12)$$

$$r^2 = 0.760$$

and for defeathered hatchlings

$$R_{\text{tot},d} = 96.4 M^{-0.558 \pm 0.0975} \quad (13)$$

$$r^2 = 0.901.$$

The ratio of $R_{\text{tot},f}$ and $R_{\text{tot},d}$ gives an indication of the relative efficacy of the downy coat in reducing

heat loss. This ratio was greater than unity for the entire range of hatchling sizes, and also was dependent upon mass. For the hatchlings

$$R_{\text{tot},f}/R_{\text{tot},d} = 1.10 M^{0.185 \pm 0.105} \quad (14)$$

$$r^2 = 0.464.$$

One can infer that the critical radius may occur where the ratio $R_{\text{tot},f}/R_{\text{tot},d}$ is unity.

Extrapolating from equation (14), this should occur at a body mass of 0.60 g with 95% confidence limits from 0.30 to 0.72 g body mass.

INSULATION AND BODY SIZE IN NEONATAL BIRDS

For both mammals and birds, altricial neonates generally are smaller than precocial neonates (Case, 1978). Also, naked skin and altriciality usually occur together. Consequently, naked neonates are in general smaller than insulated neonates. Balmer and Strobusch (1977) sought to explain the correspondence between small size and the absence of insulation as a result of the critical radius effect. The critical size, by their estimate, was 4–7 g. Naked neonates are in general smaller than 4 g, while insulated neonates usually are larger. This was felt to be compelling evidence supporting their hypothesis.

This claim also is readily testable by examining in detail what the correspondence is between body size and the presence or absence of insulation among a large group of homeotherms. We have chosen the North American birds for analysis.

Table 1. Estimated mass of hatchlings (M , g) for 443 species of North American birds, compared between types of hatchling

Type of hatchling	Altricial sparse down	Altricial naked	Altricial downy	Precocial downy
Numer of species	94	64	118	167
Mean M	2.87	8.45	17.50	29.53
Maximum M	64.74	89.45	161.03	201.38
M at 75th percentile	2.74	5.82	25.70	37.31
M at 50th percentile	1.46	3.05	6.19	20.36
M at 25th percentile	1.04	1.32	1.61	11.24
Minimum M	0.36	0.26	0.45	3.64

Information on average egg sizes and the presence or absence of insulation on the hatchlings is compiled in Harrison (1978). Egg volume (V , cm^3) is readily calculated from the lengths (L , cm) and breadths (B , cm) reported in Harrison (1978) and from an equation derived from information in Hoyt (1976)

$$V = 0.511 (L B^2)^{0.991} \quad (15)$$

Mass of the eggs may be calculated from the average density of bird's eggs (approximately 1.038 g cm^{-3} ; Paganelli *et al.*, 1974). Hatchling mass is then estimated as roughly 65% of the egg mass (Heinroth, 1922).

Estimated hatchling masses for several species of North American birds were compared for the five types of hatchlings designated by Harrison (1978): precocial and downy; semi-precocial and downy; altricial and downy; altricial and sparse down; altricial and naked. The analysis showed the estimated masses for precocial and semi-precocial hatchlings to be statistically indistinguishable; hence, data for these groups are reported as a single group: precocial and downy. Distributions for each group of hatchlings are reported in Table 1. Distributions of hatchling mass departed significantly from normal. Thus, comparisons between different types of hatchlings were made using the Kruskal-Wallis test on the ranked values of mass (Sokal and Rohlf, 1969). The mean size of hatchling for each group is significantly different from that of each of the other groups.

Table 2. Estimated numbers of species from Table 1 with hatchlings smaller than the critical sizes predicted by Balmer and Strobusch (1977) and in this study [equation (14)]

Critical sizes predicted by Balmer and Strobusch				
Type of hatchling	Altricial sparse down	Altricial naked	Altricial downy	Precocial downy
Number of species with hatchlings smaller than 6.70 g	89	50	60	1
Number of species with hatchlings smaller than 3.79 g	81	41	53	0
Critical sizes suggested by this study				
Type of hatchling	Altricial sparse down	Altricial naked	Altricial downy	Precocial downy
Number of species with hatchlings smaller than upper 95% confidence limit (0.72 g)	2	11	2	0
Number of species with hatchlings smaller than lower 95% confidence limit (0.30 g)	0	3	0	0

According to Balmer and Strobusch (1977), the critical size in still air for a cylindrical hatchling should be about 3.79 g, and for a spherical hatchling in the same conditions, it should be about 6.70 g. This is not evident in the distributions of body size among the different groups of hatchlings (Table 2). It is true that few or no downy and precocial hatchlings are smaller than 4–7 g. However, it is not possible to say there are few downy hatchlings smaller than this. Among the altricial hatchlings, there are many species with downy hatchlings smaller than 4–7 g—indeed, there are more species with downy hatchlings smaller than these predicted critical sizes than there are species with naked hatchlings (Table 2).

Extrapolation from our results on quail hatchlings (Fig. 3) suggested a critical size of about 0.6 g [equation (14)]. Most species smaller than this indeed are very small (Table 2). One still must explain the naked condition of the many species of birds that are naked and larger than these estimated critical sizes (83–95% of the total number of naked hatchlings; Table 2). In this case, it seems that the critical radius effect is not a very good explanation for the naked condition among hatchlings of small altricial birds.

DISCUSSION

The suggestion that the naked condition of many small neonatal mammals and birds can be explained by the critical radius effect is flawed on at least two counts. First, the critical size of 4–7 g predicted by Balmer and Strobusch (1977) appears to be a substantial overestimate, by at least an order of magnitude [Fig. 3; equation (14)]. Second, the patterns of insulation and body size among the North American birds in no way suggest a critical size at 4–7 g, or even at our estimate of about 0.6 g (Table 2). It might be argued that this is not a robust test of the prediction; Balmer and Strobusch (1977) were concerned explicitly with homeotherms. The presence or absence of insulation on altricial hatchlings, which probably are not homeothermic, therefore might be construed as irrelevant. When applied to precocial hatchlings, which probably are homeothermic, the prediction holds up—there are very few downy and precocial birds smaller than about 4 g (Table 2). A more relevant test for altricial hatchlings might therefore examine the correspondence between body size and insulation at the onset of endothermic homeothermy. This line of argument will not stand up, however. First, there is no evidence that the critical size actually is 4–7 g body mass. Second, the mass of altricial hatchlings at the onset of endothermy is not uniform, as the view of Balmer and Strobusch (1977) might suggest, but rather is highly variable (Dunn, 1974). Finally, the appearance of feathers on altricial hatchlings bears little relation to the onset of endothermy (Dawson and Evans, 1960; Marsh, 1979).

While the critical radius effect cannot explain such attributes as the minimum size for insulation, or the minimum possible size for endothermy in an insulated animal, it is possible that it is relevant in some way to the energetics of very small animals. A few bird hatchlings are smaller than our estimated

value of a critical size of 0.6 g (Table 2), and some insects that are facultatively endothermic are as small as this (Gunn, 1942; Heinrich, 1981).

In this regard, it is noteworthy that the critical size we suggest is an extremely generous estimate, probably close to the maximum size it could be. If a critical size exists at all, it probably is much smaller. Our experiments were in still air, with little radiation heat exchange. Thus, external heat transfer coefficients were as small as they probably ever would be. Larger external heat transfer coefficients, as would be expected for a higher wind speed past the animal, or a greater exchange of radiant energy would result in a critical radius smaller than our estimate [equation (10)]. Animals cannot reasonably be expected to usually be in still air or in conditions where radiation exchanges of heat will be very small. It is legitimate to ask then if *any* animal would ever be smaller than the critical radius. Indeed, the insulation even on very small insects (0.5 g and up) retards heat loss (Casey and Hegel, 1981; Heinrich, 1981).

One final point is worth exploring. The physical theory behind the critical radius is straightforward, and in applying it to the problem of insulation in newborn homeotherms, Balmer and Strobusch (1977) limited it in appropriate ways, and used well-accepted values for the thermal conductivity of a layer of fur or feathers. It is worthwhile to then ask—why was their estimate so unrealistic?

One possible answer concerns the assumption that the insulation layer is homogeneous in its thermal properties. This may be a good assumption for furs or down laid out on a flat surface, which is the condition for most experimental studies of animal insulation. Homogeneity of insulation may not be such a good assumption when it is on a highly curved surface, as might be expected on the body of a small animal—shafts of insulation that may have been more or less parallel on a flat surface probably no longer will be on a highly curved surface. If this either reduces the thermal conductivity of the insulation layer (unlikely), or increases the external heat transfer coefficient (more likely), the result will be a smaller critical radius than predicted for a homogeneous insulator [equation (14)].

The extrapolation of equation (14) to a critical radius of about 0.6 g supports this idea. However, our extrapolation suffers from the problems of all extrapolations—it is not to be trusted. An inhomogeneous insulator may invalidate the theory of the critical radius, with the consequence that a critical radius may not exist at all. Some recent theoretical work on heat exchange in pelage suggests this may be true (Porter *et al.*, 1985).

Whichever is the correct view, the failure of the critical radius theory to estimate the critical size of insulated animals suggests that the flows of heat through fur or feathers may be governed in quite

different ways when they are on highly curved surfaces than when they are on relatively flat surfaces.

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