

# ADAPTATION TO COLD IN ARCTIC AND TROPICAL MAMMALS AND BIRDS IN RELATION TO BODY TEMPERATURE, INSULATION, AND BASAL METABOLIC RATE \*

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In two previous papers<sup>5</sup> we showed how climatic adaptation of arctic and tropical mammals and birds was clearly manifested by their widely different critical gradients. The critical gradient was defined as the largest temperature difference between the body interior and the air that an animal can stand without losing body temperature, when the metabolism is basal.

It was pointed out that the critical gradient in an insulated thermoregulated system depends upon the product of the over-all insulation and the basal metabolic rate. This leaves the animals with three possible main avenues for adaptation to cold, namely (1) the body-to-air gradient, (2) the insulation, and (3) the basal metabolic rate, and it is our task in the present paper to estimate quantitatively the importance of each of these factors for climatic adaptation. For this purpose we must first know more precisely what thermal stresses animals are faced with in their arctic and tropical climate.

## THE THERMAL ENVIRONMENT

The temperature conditions at Point Barrow and at Barro Colorado are about as different as could be found. Records shown in Table I indicate that on the arctic coast annual extremes may differ by 65°. Inland or in exceptional years on the coast the difference may be 80°–90°.

At Barro Colorado the temperature in a shaded location near the ground is extremely constant and seldom varies from 28° C. Tropical microclimates, on the other hand, vary considerably, as is shown by observed diurnal variations with altitude in the forest at Barro Colorado. In February the diurnal variation at ground level was 6.5°, at a 55 foot height 9.5°, and at an 86 foot altitude 16.5° (Allee, 1926). The mean maximum-minimum range at ground level is 2.9° and in the canopy 11.8° or four times greater.

On first consideration we would expect an arctic mammal to be cold adapted and a tropical mammal to be heat adapted. It is quite obvious that the arctic mammals are adapted to withstand cold or they would freeze to death. If we consider, how-

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<sup>5</sup> Many problems touched upon in this and the foregoing papers have been discussed in the stimulating paper "The application of the theory of heat flow to the study of energy metabolism" by Burton (1934).

ever, that fur always conserves heat and that most tropical mammals are fur covered, then we realize that conservation of heat, *i.e.*, adaptation to cold, is also a conspicuous feature in tropical mammals. We may say then that an arctic mammal is adapted to cold and a tropical mammal to less cold. That this is true is evident if we consider the critical gradients. Several of the tropical mammals examined have a critical temperature between 25° C. and 27° C. which is only 10° below their body temperature. If the air temperature drops only a few degrees lower they begin to shiver from cold, and if it were to rise only 9° above their critical temperature they would have to increase their heat dissipation ten times to keep in heat balance. Such changes in environmental temperature do, however, take place between day and night in the tropics (Allee, 1926). In contrast to this an arctic mammal at its critical temperature of -40° C. to -45° C. can adjust to 0° C. merely by halving the insulation. Such large changes in the environmental temperature are seasonal rather than diurnal, however, and are compensated for by seasonal changes in insulation (shedding).

It seems then that the problem for tropical mammals is neither overheating nor cooling but, actually, both. Their low critical gradient, whether due to low insulation or low metabolism, gives them a very small range of temperature tolerance in

TABLE I

*Temperature reported at Barrow, Alaska (lat. 71°) in 1948, converted to centigrade degrees (from climatological data, Alaska, 1948)*

|         | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---------|------|------|------|------|-----|------|------|------|-------|------|------|------|
| Average | -28  | -24  | -27  | -17  | -10 | -1   | 5    | 2    | -4    | -12  | -21  | -29  |
| Minimum | -38  | -42  | -43  | -32  | -26 | -10  | -2   | -5   | -15   | -26  | -40  | -43  |
| Maximum | -5   | -4   | -13  | 1    | 0   | 4    | 22   | 14   | 5     | -2   | -2   | -8   |

both directions. The heat of the day, rain and storm, and the cool of the night will frequently exceed their narrow zone of thermoneutrality and in short succession they may be subjected to both cold and heat. The same is often experienced by man in the tropics. The days may be extremely hot even with a minimum amount of clothing, and a night without extra clothes can be very chilling. What then should a tropical mammal adapt for, overheating in day or cooling at night? The fact that most of them are well furred shows that they do adapt to cold. By what means and to what extent they can protect themselves against heat, we have not studied quantitatively. Some of them do it by sweating and panting, many avoid the sun by seeking shade, and many are inactive during the heat of the day; some resort to the water for cooling. It would seem that gains in latitude of heat regulation would be an advantageous adaptation to a tropical climate.

We pointed out above how cold sensitivity would depend upon three main factors: (1) the body-to-air gradient, (2) the insulation, and (3) the basal metabolic rate.

#### BODY TEMPERATURE AND CLIMATIC ADAPTATION

We shall first consider the body-to-air gradient in relation to climatic adaptation. As the heat loss is proportional to the gradient, other factors being equal, arctic mam-

mals would gain in heat conservation by having a lower body temperature than other mammals, and tropical mammals would gain in latitude of heat regulation if they were warmer than usual.

We saw in the preceding papers that all arctic mammals and birds so far tested have an internal body temperature like the temperate forms, and actually they would gain very little in heat preservation from a low body temperature unless it were considerably lower than normal. A body temperature of 30° C. instead of 37° C. would, at -40° C. air temperature, save only 10 per cent of the rate of heat loss. The large lowering of the body temperature during hibernation combined with an insulated nest does, however, reduce the gradient and the heat loss considerably, but it occurs only in dormant animals. The smaller arctic mammals and man could not maintain inactive resting periods without lowering the gradient, however, and they can only do this if they raise the external temperature by providing themselves with added insulation in the form of nests and clothing. It is interesting to note that "behavioral thermoregulation" has also been found to be characteristic for all reptiles thus far studied (Bogert, 1949).

There are no tropical mammals or birds known to have body temperatures higher than usual (Wetmore, 1921; Wislocki, 1933), and consequently none of them have a heat adapted body temperature. Quite a few normally have a low body temperature, however, *e.g.*, sloths, armadillos, anteaters (Wislocki and Enders, 1935), and monotremes (Martin, 1902). Lowered body temperature *per se* makes them a little more cold hardy, but at the same time more sensitive to changes in the air temperature because of the lowered critical gradient. They gain some latitude, however, by the fact that they are all poor temperature regulators. This is a condition well known in bats and other hibernators from all climates and represents traces of a thermal survival latitude characteristic of poikilotherms. It has nothing to do with an adaptive change of body temperature to a new and constant level such as we would expect in a truly homoiothermic animal. We may state then that there are no signs so far that body temperature of mammals and birds is adaptive to the different climates on earth. A logical corollary of this is that it cannot have been adaptive to the over-all climatic conditions on earth either. It seems then that the narrow band of body temperature on which both birds and mammals operate is a fundamental, nonadaptive constant in their biochemical setup. It can be kept constant only within certain climatic limits which are determined by the latitude of the physical and chemical heat regulation of the animal. Whereas mammals and birds undoubtedly could adapt to colder climates than we have today by increasing their insulation, they are very near their upper limit in a warm tropical climate. Many parts of the tropics are so hot and humid that a few degrees' rise in the temperature would mean death for mammals and birds because they cannot adapt to it by raising their body temperature.

In contrast to the inadaptability of the internal body temperature, peripheral parts may show a great deal of temperature adaptation, such as the cold extremities of aquatic mammals and birds.

#### INSULATION AND CLIMATIC ADAPTATION

Having eliminated the internal body temperature as an adaptive factor in arctic and tropical mammals, there remains the insulation and the basal metabolism to ac-

count for the striking differences which we have observed in their sensitivity to cold. It is, of course, common knowledge that the mammalian body insulation is highly adaptive to climate, phylogenetically as well as ontogenetically. We saw that the mammalian species of cold climates have, in general, much warmer fur than those of warm climates; that there are adaptive seasonal changes (moulting), and it is known that, for instance, dogs (v. Hoesslin, 1888) and rabbits (Mayer and Nichita, 1929) can be experimentally induced to increase their insulation if exposed long enough to cold. There is no reason to believe that the arctic climate is so cold that the larger mammals cannot produce adequate insulation against it but must resort to a high metabolism. They could certainly grow and wear much longer and warmer fur if they needed to, *i.e.*, a 500 kg. moose would not need to stop at the insulation of a 5 kg. fox.

In a previous paper we substantiated, by insulation measurements, the general rule that arctic mammals have warmer furs than do the tropical mammals. We found, however, some striking exceptions to this. For instance, the little arctic weasel, although much cold hardier, possesses only half the fur insulation of the tropical sloth. We pointed out that the explanation was to be found in the difference in the heat production of the two animals. The cold legs of arctic aquatic birds and mammals (and probably of the terrestrial forms as well) may be taken as another example of adaptive insulation.

#### BASAL METABOLIC RATE AND CLIMATIC ADAPTATION

As pointed out by Rubner (1883), Richet (1891), Voit (1901) and others, practically all mammals so far investigated show a nearly linear relation between the basal heat production and the body surface, usually estimated according to Meeh's formula as  $K \times \text{Weight}^{2/3}$ . They were found, in other words, to have approximately the same rate of heat dissipation per surface unit, or to follow the "surface law" of Rubner. The material was later amplified by Benedict (1938) in his famous mouse to elephant curve, and it was realized that the correlation came closer to  $K \times \text{Weight}^{3/4}$  (Kleiber, 1932, 1947; Brody and Procter, 1932), which does not have the meaning of a surface area, although it is numerically almost the same except at the extremes of size. The fact that a near surface relation between body size and basal metabolic rate holds also for many groups of cold-blooded animals (Weymouth, Crismon, Hall, Belding and Field, 1944) is a clear indication that this relation is fundamental and is not primarily caused by heat loss (Terroine and Delpech, 1931; Krogh, 1941; Zeuthen, 1947).

From Benedict's mouse to elephant curve it is indicated that the basal metabolic rate is determined by body size, irrespective of climate. If this is so, however, and the body temperature is constant, then we may conclude that the only factor left to take care of climatic adaptation is insulation. Without further evidence we cannot preclude, however, that one might still find different adaptive metabolic levels in animals living under such extremes as the arctic and the tropics. A higher heat production, other factors being equal, would make an animal cold-hardier, and a lower heat production heat-hardier, and it is of interest therefore to know the metabolic rate of our animals in absolute units as compared with animals from less extreme climates.

In Figures 1 and 2 we have plotted our arctic and tropical mammals on the stand-

ard mouse to elephant curve, drawn according to the equation  $\text{Cal./per day} = 70 \text{ kg.}^{3/4}$ . The metabolism has been calculated from the oxygen consumption (arctic) or the  $\text{CO}_2$  production (tropical), assuming an RQ of 0.80, and a caloric equivalent of one liter of oxygen = 4.8 Calories. Generally when such determinations are made the animal is confined in a cage but can move about during the experiment if it so wishes. Even if active runs are weeded out, the strict prerequisites for a basal determination as in man rarely apply. However, we believe that our determinations fall in line with most other determinations of the basal energy level in wild animals, with the added advantage that we know definitely that each determination was made in the thermoneutral zone. Most of our determinations were started in the morning, the larger animals having fasted over night, the smaller ones for a couple of hours.

From Figure 2 we see that our adult arctic mammals, lemmings, ground squirrels, and foxes all line up closely with the standard curve, but the weasels do not. Since the larger arctic mammals (from a 5 kg. fox to a 500 kg. moose) have about the same

KG CAL / 24 HOURS

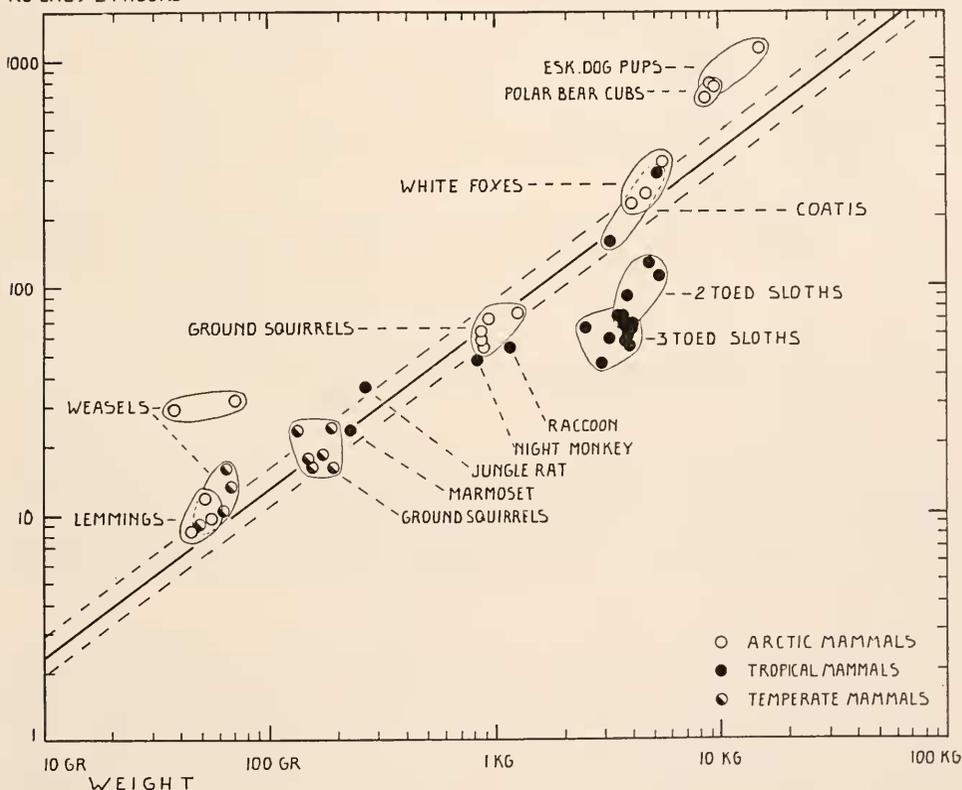


FIGURE 1. Basal metabolic rate in relation to body size. Full drawn line is the mouse to elephant curve drawn according to the equation  $\text{Kg. Cal./day} = 70 \times \text{kg.}^{3/4}$ . Dotted parallel lines are 20 per cent deviations. Besides our own material the following has been used: ground squirrels (Erikson, 1950; and Gelineo, 1939), sloths (Ozorio de Almeida and Branca de Fialho, 1924; Irving, Scholander, and Grinnell, 1942), least weasels from Wisconsin (Morrison, unpublished).

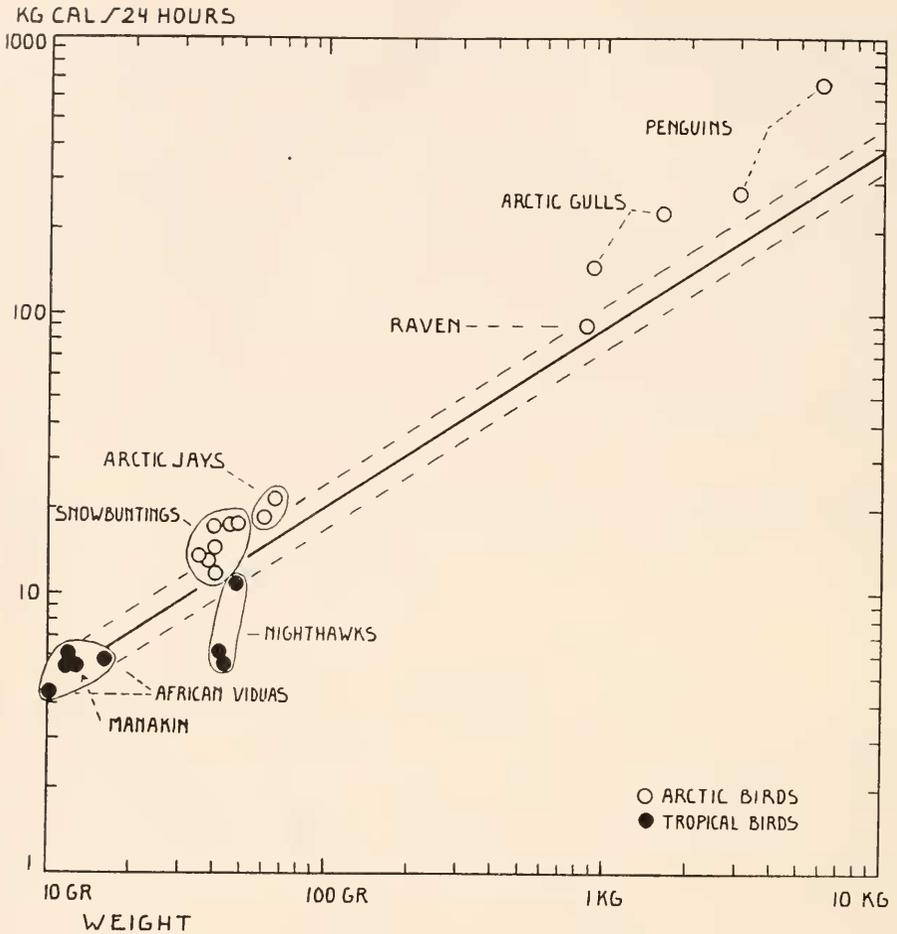


FIGURE 2. Basal metabolic rate in relation to body size. Full drawn line represents the curve given by Brody (1945) for birds according to the equation  $\text{Kg. Cal./day} = 89 \times \text{kg}^{0.64}$ . Dotted parallel lines are 20 per cent deviations. The African *Vidua paradisea* are taken from Terroine and Trautmann (1927), the antarctic penguins (*Pygoscelis papua* and *Eudyptes chrysotophus*) from Scholander (1940). The raven was kept most of the time as a pet in the laboratory building ( $-5^{\circ}\text{C. to }+25^{\circ}\text{C.}$ ).

fur insulation per unit surface, and since they are subjected to the same climatic temperature gradients, it follows that their heat loss will be roughly proportional to their surface area. Since the fox falls on the mouse to elephant line it is therefore likely that all the larger arctic mammals do also. We see further that the tropical mammals, excepting the two species of sloths, likewise fall on the line. If we realize furthermore that the mouse to elephant curve already is based on animals ranging from relatively cold-hardy temperate rabbits to tropical elephants we may state as a tentative generalization that the basal metabolic rate of terrestrial mammals from tropics to arctic is fundamentally determined by a size relation according to the

formula  $Cal./day = 70 kg.^{3/4}$ , and is phylogenetically nonadaptive to external temperature conditions. Equally nonadaptive is the body temperature, and the phylogenetic adaptation to cold therefore rests entirely upon the plasticity of the factors which determine the heat loss, mainly the fur insulation. Small adaptive changes cannot, of course, be detected by such interspecific comparisons as these. There is also, however, intraspecific evidence from observations on man, which have failed to reveal any certain racial metabolic or body temperature adaptations to cold climates (DuBois, 1936). Man and animal alike do it all with insulation.

Our weasels were adults and had a metabolic rate two to three times higher than that expected from the standard curve. There are indications that our weasel figures are representative. The figures are averages of the lowest of several determinations in which the weasel was seen to be lying down curled up. Furthermore, during cold experiments they mobilized a heat production nearly four times larger than basal, which is as high as any other animal could maintain for long periods in a small cage. Finally, as we shall see, the high metabolism is a corollary to their relatively poor body insulation. Dr. Peter R. Morrison has kindly informed us that the average minimum value from runs on two individuals (*Mustela vison*) from Wisconsin showed only a slight elevation above the standard curve (Fig. 1). Hence we are forced to conclude that our arctic weasels had a greatly increased resting metabolic rate compared with the southern form. This may possibly mean a metabolic adjustment to cold. If the cold were the direct reason for the high resting rate it seems somewhat odd that the fur is so slight; presumably it could easily have been doubled!

We must still account for the fact that some tropical mammals have a very low metabolic rate, notably the sloth and possibly the armadillo. The sloth is clearly adapted to cold because of its warm fur, which acts compensatory to its low metabolism. Its low body temperature is likewise heat conserving. Low metabolism combined with low or labile body temperature is found also in non-tropical mammals, e.g., marmot (Benedict, 1938), bats (Hock, 1949) and others and has scarcely anything to do with climatic adaptation but is rather tied up with the hibernation reaction which occurs in all climates.

In birds we do not know the relation between basal metabolic rate and weight as well as in mammals. In Figure 2 our few arctic and tropical birds have been plotted upon the standard exponential curve given by Brody (1945), based on domestic birds (hens, pigeons, sparrows, canaries). The snow buntings migrate south in the winter and their high critical temperature (+ 10° C.) indicates that they were under continuous cold stress during all of the winter at Point Barrow. Nevertheless their basal metabolism was not elevated. Our two gulls were high, and normally they also migrate to warmer climates in the winter. In a series of large birds, Benedict and Fox (1927) found the highest figures for pelicans and gulls. Scholander (1940) found high figures for penguins, and many aquatic mammals are also high (Fig. 3). In Benedict and Fox a series of large birds from the New York Zoological Park includes many tropical species and they fall near the standard line, together with the temperate birds. Two of our night hawks are very low, and this is probably due to their faculty of hibernation. More material is necessary before we can tell whether the basal metabolism in birds may be adaptive to climate.

It should be pointed out that ontogenetic adaptations of the basal metabolic rate

to cold have been induced experimentally in several species of mammals and birds (Gelineo, 1934, 1939; Schwabe, Emery and Griffith, 1938; Ring, 1939; Lee, 1942). The rise is generally below 20 per cent, but can get up to 50 per cent, and depends upon the length of exposure and the degree of cold. It is not clear whether the rise would be permanent. It would seem likely that in some animals at least, within reasonable limits and given enough time, the insulation would take over the whole adaptation, permitting the metabolism to drop back to normal. In any case a mere 50 per cent increase in the metabolic rate is an ineffective and expensive adjustment to a gradient which may have changed 10 times or more! We did not find a high basal metabolic rate in pigeons which had been kept for four months at Point Barrow at 0° C. to -40° C. air temperature.<sup>6</sup> Dugal and Thérien (1947) found that rats and guinea pigs needed large quantities of ascorbic acid to adapt to cold, *i.e.*, to thrive and grow at a body-to-air gradient which was two to three times larger than

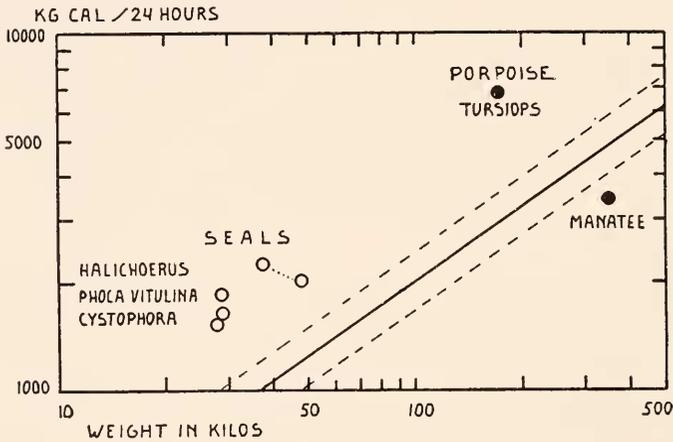


FIGURE 3. Basal metabolic rate in relation to body size in some aquatic mammals. Full drawn line is mouse to elephant curve, with 20 per cent deviation lines dotted (cf. Fig. 1). The seal records are taken from Irving, Solandt, Solandt, and Fisher (1935) and Scholander (1940), the porpoise from Irving, Scholander, and Grinnell (1941), and the manatee from Scholander and Irving (1941).

that of the control animals. The cold-adapted animals consumed only about 40 per cent more food than the controls, however, and it therefore seems that the major factor in their cold adaptation must have been a decrease in their heat dissipation. The diminished heat loss could have been due to growth of more fur, establishment of colder and deeper tissue gradients, difference in posture, etc.

Very feeble seasonal changes of basal metabolism ( $\pm 5$  per cent) have been observed in pigeons (Dontcheff and Kayser, 1934) which may, however, have been caused by factors other than temperature. In the regular and fully developed seasonal adaptation to cold which we see in our wild species, it seems likely that the

<sup>6</sup> Pigeons are known to stand considerable cold (Horvath, Folk, Craig and Fleischmann, 1948) and a number of them were kindly sent to us from Edgewood, Maryland, at the suggestion of Dr. David Bruce Dill.

insulation is normally responsible for the whole temperature adaptation. Ontogenetic changes in the basal metabolic rate of man, induced by seasons or transfer to hot or cold environment, are small and difficult to interpret (DuBois, 1936; Ames and Goldthwait, 1948); man does it mainly by insulation.

#### THE RELATION OF COLD HARDINESS TO INSULATION AND BASAL METABOLISM

The adherence of mammals from all climates to the mouse to elephant curve holds astonishingly well in general, but there are marked exceptions. It applies only to adult animals, young ones being generally high (cf. Brody, 1945, p. 406). This undoubtedly is the explanation for the high basal rates of our very young polar bear cubs and husky pups. There are also well known examples of animals with substandard metabolic rate, notably the marmot (Benedict, 1938) and the sloth (Ozorio de Almeida and Branca de Fialho, 1924).

For all these animals, whether their metabolic rate falls on the standard line or not, heat output must balance the heat production, provided they maintain the body tem-

TABLE II

*Basal metabolism of some arctic and tropical mammals and birds*

The basal rate (BM) is the lowest range of the resting rates (RM) given in Figures 4, 5, and 6 of preceding paper  
 $BM = f \times RM$

| Species           | Weight grams | f    | BM kg. cal./24 hrs. | Species          | Weight grams | f    | BM kg. cal./24 hrs. |
|-------------------|--------------|------|---------------------|------------------|--------------|------|---------------------|
| Arctic mammals    |              |      |                     | Arctic birds     |              |      |                     |
| Dog (pups)        | 14,500       | 0.85 | 1,140               | Gull             | 1,600        | 1.0  | 304                 |
| Dog (pups)        | 9,000        | 0.85 | 930                 | Raven            | 850          | 1.0  | 92                  |
| Polar bear (cubs) | 9,300        | 1.00 | 750                 | Pigeon, domestic | 510          | 1.0  | 33                  |
| Polar bear (cubs) | 8,500        | 1.00 | 690                 | Pigeon, domestic | 400          | 1.0  | 28                  |
| White fox         | 5,500        | 0.85 | 353                 | Pigeon, domestic | 375          | 1.0  | 47                  |
| White fox         | 4,600        | 0.85 | 268                 | Pigeon, domestic | 300          | 1.0  | 49                  |
| White fox         | 4,000        | 0.85 | 234                 | Pigeon, domestic | 400          | 1.0  | 49                  |
| Ground squirrel   | 1,250        | 0.70 | 77                  | Alaska jay       | 65           | 1.0  | 22                  |
| Ground squirrel   | 940          | 0.70 | 72                  | Alaska jay       | 62           | 1.0  | 18                  |
| Ground squirrel   | 880          | 0.70 | 55                  | Snow bunting     | 35           | 0.75 | 14                  |
| Ground squirrel   | 880          | 0.70 | 67                  | Snow bunting     | 48           | 0.75 | 18                  |
| Ground squirrel   | 870          | 0.70 | 59                  | Snow bunting     | 38           | 0.75 | 13                  |
| Weasel            | 70           | 0.85 | 31                  | Snow bunting     | 48           | 0.75 | 18                  |
| Weasel            | 38           | 0.85 | 29                  | Snow bunting     | 40           | 0.75 | 17                  |
| Lemming           | 56           | 0.9  | 9.6                 | Snow bunting     | 40           | 0.75 | 14                  |
| Lemming           | 52           | 0.9  | 12                  | Snow bunting     | 40           | 0.75 | 12                  |
| Lemming           | 45           | 0.9  | 8.8                 |                  |              |      |                     |
| Tropical mammals  |              |      |                     | Tropical birds   |              |      |                     |
| Coati             | 5,100        | 1.0  | 335                 | Night hawk       | 43           | 1.0  | 7.7                 |
| Coati             | 3,200        | 1.0  | 163                 | Night hawk       | 43           | 1.0  | 7.6                 |
| Two-toed sloth    | 3,770        | 1.0  | 71                  | Night hawk       | 49           | 1.0  | 13                  |
| Raccoon           | 1,160        | 1.0  | 53                  | Manakin          | 12           | 1.0  | 6.4                 |
| Night monkey      | 820          | 1.0  | 48                  |                  |              |      |                     |
| Jungle rat        | 265          | 1.0  | 39                  |                  |              |      |                     |
| Marmoset          | 225          | 0.9  | 27                  |                  |              |      |                     |

perature constant, and we should expect that animals with the same critical gradient, living under the same climatic conditions, would show an inverse relation between the metabolic rate and the insulation according to the formula  $\Delta TC = \text{Insulation} \times \text{basal metabolism}$ . If we compare our weasels with the "standard" lemmings (Fig. 1) we see that the weasels have two to three times as high basal rate, but only half the insulation, and we may therefore say that the weasel requires less insulation *because* its metabolism is so high. Our little polar bear cubs and husky pups were observed to have much shorter fur than the adults, and evidently needed less insulation *because* of their high metabolic rate.

The sloth, with less than half the standard metabolism, has a fur nearly twice as warm as other tropical mammals (for instance, the coati) but even so its metabolism is barely enough to keep it warm, as evident from its extreme temperature sensitivity.

TABLE III

*Critical gradients ( $\Delta TC$ ) observed from respiration curves compared with gradients calculated from measurements of fur insulation and basal metabolism (all temperatures centigrade)*

| Arctic species         | White fox  | Weasel | Lemming    | Ground squirrel (Summer) |
|------------------------|------------|--------|------------|--------------------------|
| Observed $\Delta TC$   | 80°        | 22°    | 20°        | 20°                      |
| Calculated $\Delta TC$ | 68, 82, 70 | 40, 27 | 13, 13, 18 | 17, 18, 19               |

| Tropical species | Coati | Jungle rat | Marmoset | Night monkey | Raccoon | Two-toed sloth | Three-toed sloth |
|------------------|-------|------------|----------|--------------|---------|----------------|------------------|
| Obs. $\Delta TC$ | 15    | 14         | 13       | 10           | 9       | 8              | —                |
| Cal. $\Delta TC$ | 13    | 8          | 11       | 11           | 5       | 9, 10, 7, 8    | 6, 6, 9, 5       |

It seems that another tropical mammal, the armadillo, evidently can have a basal metabolic rate as low as that of the sloth, although it is almost naked. Ozorio de Almeida and Branca de Fialho (1924) found practically normal basal rates in six specimens, and Scholander, Irving and Grinnell (1943) found only half of that rate in three specimens of the same species. Whatever the reason for this latitude in basal rate, we may observe that the armadillo is conspicuously chubby, presenting a low surface area compared with the long-armed and long-legged sloth. It is also relatively heavier due to its bone armor and the two species are not comparable in regard to microclimatic environment, for the armadillo with its burrowing habit does not live as exposed to the weather as does the arboreal sloth. Allee (1926) found four times less temperature variation at ground level in the jungle of Barro Colorado than in the canopy 86 feet above ground level, and it may be that arboreal mammals, on the whole, have warmer fur than the terrestrial forms in these parts of the tropics.

From our insulation and metabolism measurements it is theoretically possible to make an estimation of the critical gradient appropriate to the different animals, provided that the fur insulation is maximal and provided we can get a rough estimate of the surface area of the animal. If we know the rate of heat transfer through a given fur area at a one degree gradient, and we find that  $T$  times as much heat passes

through the same area when the fur is on the animal, then we know that the gradient is  $T$  degrees, provided that other factors remain constant.

We know the heat transfer per unit surface area and per degree from our insulation measurements and we know the total heat loss through the basal metabolism determinations; the surface can be approximated roughly by using Meeh's formula,  $0.1 \times \text{Weight}^{2/3}$ , which gives the approximate surface in  $m^2$  when weight is expressed in kg. Accordingly we find the critical gradient is equal to:  $\frac{\text{Cal./24H}/0.1 W^{2/3}}{\text{Cal./24H}/m^2/1^\circ\text{C.}}$ .

We see from Table III that the critical gradient, as calculated from insulation and metabolism, gives a fair correlation with the observed critical temperature of the tropical and arctic mammals. The relative order is fairly well represented and the absolute magnitudes of the gradients come out surprisingly well.

#### SUMMARY

Maintenance of constant body temperature in a homoiothermic animal depends upon a balance between heat production and heat dissipation, and there are consequently three possible main avenues for climatic adaptation, (1) by body-to-air gradient, (2) by heat dissipation, and (3) by metabolic rate. There is no evidence of adaptive low body temperature in arctic mammals and birds, or high body temperature in tropical mammals and birds. The body-to-air gradient can be adapted only by means of behavioral thermoregulation (nest building, avoidance of direct sunshine, etc.). With few exceptions our adult arctic and tropical mammals and birds have a basal metabolic rate that fits the standard mouse to elephant curve, *i.e.*, the basal metabolic rate is determined by an exponential relation to size, evidently fundamental to most animals, warm-blooded or not. The basal metabolic rate is consequently not influenced by such factors as temperature gradient and insulation which largely determine the heat loss, and is hence inadaptive to climate. Equally inadaptive is the body temperature, and the phylogenetic adaptation to cold or hot climate therefore has taken place only through factors that regulate the heat dissipation, notably the fur and skin insulation.

For any temperature gradient where the body temperature is maintained, the over-all insulation and the metabolic rate must be so adjusted that their product is proportional to the gradient. This is confirmed by our material inasmuch as the observed critical gradients can be approximately predicted from fur insulation and basal metabolic rate. Under the same climatic conditions there may be an inverse relation between metabolic rate and fur insulation.

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