

COMPARATIVE PHYSIOLOGY OF TEMPERATURE REGULATION

PART 3

Editors

JOHN P. HANNON
ELEANOR VIERECK



ARCTIC AEROMEDICAL LABORATORY
FORT WAINWRIGHT
ALASKA
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RESPONSES AND ADAPTATIONS OF WILD BIRDS TO ENVIRONMENTAL TEMPERATURE

George C. West

Birds maintain relatively constant body temperatures, in general several degrees higher than those of mammals, in spite of external temperatures that range for some species to above 40°C and for others as low as -60°C . The ability to maintain a constant temperature in the face of such thermal extremes is dependent upon the proper coordination and regulation of the mechanisms for heat production and heat loss. A complete understanding of these mechanisms would enable one to obtain a more thorough picture of how birds adapt to their ever changing environments in nature.

The basic principles of thermal exchange in homeotherms have been well reviewed by Hart (1957) and more recently by King and Farner (1961), who have shown that birds behave essentially as heat machines, varying heat gain and heat loss to maintain a constant temperature under all thermal conditions in which they are capable of surviving.

This review will attempt to summarize some of the recent work on the responses of wild birds to temperature, with particular emphasis on the effect of environmental temperature below body temperature and the bioenergetic adaptations of birds to temperature under natural conditions.

Body Temperature

A large number of deep body temperatures have been recorded for adult birds in almost every order (Baldwin and Kendeigh, 1932; Bartholomew and Dawson, 1954; Bartholomew and Cade, 1957; Dawson, 1954; Farner, 1956; Farner et al., 1956; Irving and Krog, 1954,

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1955, 1956; Steen and Enger, 1957; Udvardy, 1953, 1955; Wetmore, 1921; and others). The variety of methods used, however, prohibits legitimate comparison in most cases, e.g.: (1) use of a thermocouple or mercury thermometer inserted into the cloaca or proventriculus of a bird held in the hand, (2) use of a thermometer in the cloaca or proventriculus immediately after shooting, (3) use of thermocouples inserted temporarily in the cloaca, (4) use of indwelling thermocouples implanted with the junction under the skin or in the pectoral muscles. The last method will give the most satisfactory results for comparative purposes, especially when temperatures are recorded continuously in the dark at night (for diurnal species) while the bird is at a thermoneutral temperature (near 30°C) and in a post-absorptive condition (King and Farner, 1961). Deep body temperatures obtained under these conditions average about 40.3°C for passerines and 39.5°C for non-passerines.

The core temperatures of birds are relatively constant, and fluctuations in temperature are minimized. The shell, consisting of the skin, feathers, scales, subcutaneous fat, and tissue, including some skeletal muscle, acts as an insulating layer whose rate of thermal conductance can be increased when deep body temperatures rise and decreased when deep body temperatures fall. The distal unfeathered portions of the leg and foot are most important for rapid dissipation of heat (Bartholomew and Dawson, 1958), while the subcutaneous fat and feathers are important for the prevention of heat loss.

Core temperatures of adult diurnal birds increase with gross activity during the day and drop when the bird is at rest during the night. At high and constant ambient temperatures, diurnal fluctuations in body temperature are less pronounced, being about 1°C to 3°C (Bartholomew and Dawson, 1954; Dawson, 1954), while at low ambient temperatures, body temperatures may drop 3°C to 4°C at night below the normal daytime value (Fig. 1).

Temporary hypothermia has been recorded for adult birds in the Caprimulgiformes, Apodiformes and Coliiformes (Bartholomew, Howell, and Cade, 1957) and possibly in two families of the Passeriformes, the Hirundinidae (McAtee, 1947) and the Paridae (Steen,

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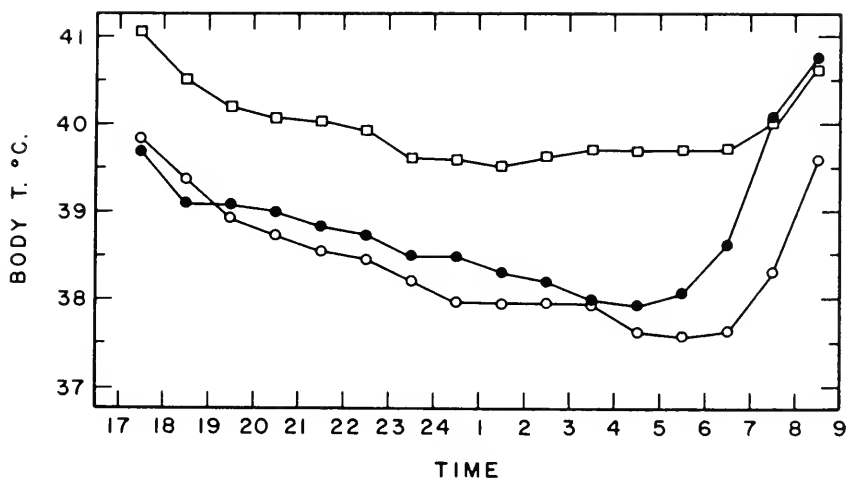


Figure 1. Body temperatures of eight Evening Grosbeaks recorded by indwelling thermocouples at a constant temperature of 30°C (□), a constant temperature of -15°C (●), and outdoors during January at -6.8°C (○).

1958). It has been observed that nocturnal hypothermia in the cold, such as that recorded by Steen, in small passerines is often due to the birds' inability to adapt to caging and experimental conditions on the first night of capture. Most birds whose body temperatures dropped more than 4°C the first night of capture lost weight or ultimately did not survive (Fig. 2).

Temporary hypothermia is common among the young of most altricial species since they are essentially poikilothermic when hatched and develop homeothermy during the nestling period (Baldwin and Kendeigh, 1932). Body temperatures of these young, therefore, are subject to considerable variation independent of activity or time of day since they are dependent for warmth on the brooding of their parents.

Heat Regulation

Physical Mechanisms. Physical thermoregulation involves alteration in the physical aspects of the shell, increased use of the respiratory surfaces as an avenue of heat loss, and changes in behavior pattern. As the temperature falls below thermoneutrality, birds gradually increase their total insulation until it reaches a maximum level, which is then maintained. According to classical theory, this increase in insulation occurs before an increase in heat production is required (Fig. 3)(Scholander et al., 1950a; Hart, 1957; King and Farner, 1961). Insulation in the cold involves vasoconstriction of peripheral vessels, increase in the insulating ability of the plumage, and behavioral adaptations such as huddling, sitting on legs and feet, "balling up" by putting the head under the wing, burrowing, or roosting in cavities (Kendeigh, 1961a). It is evident that the plumage is the major insulator, since temperatures recorded under the skin are within 0.5°C to 1.0°C of the core temperature (Steen and Enger, 1957; West and Hart, unpublished), and thermocouples placed on the skin under the feathers are also within 1°C to 2°C of the core temperature (Dawson and Tordoff, 1959).

Direct measurements of the insulating ability of the plumage are difficult to make (Scholander et al., 1950b), but calculations of

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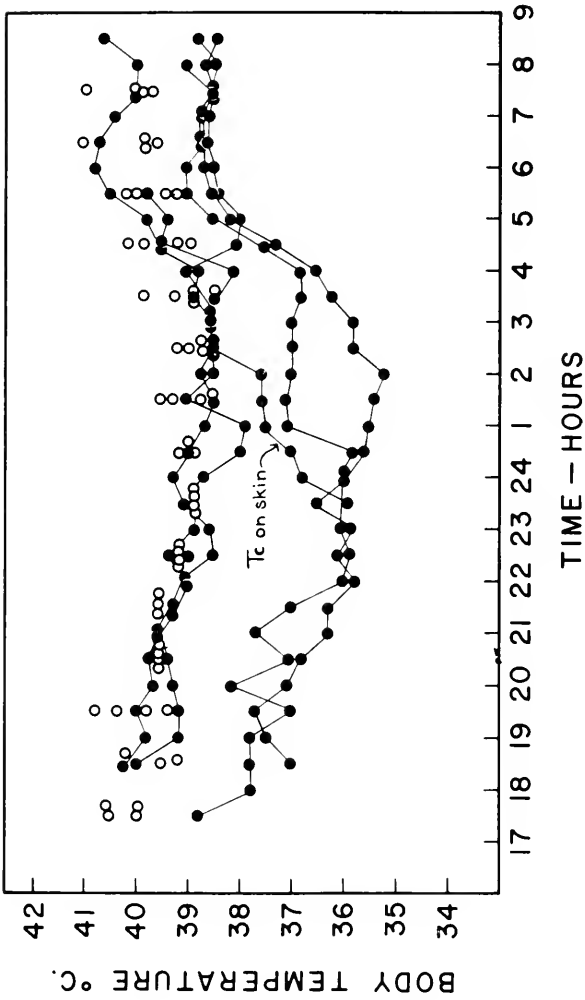


Figure 2. Body temperatures of winter acclimatized Common Redpolls recorded by indwelling thermocouples at an ambient temperature of -10°C . Records of individual birds on the night of capture in March (●) compared with four birds held in captivity out-of-doors until June and recorded at -20°C (○). The lower two records are of birds that died about 9 AM.

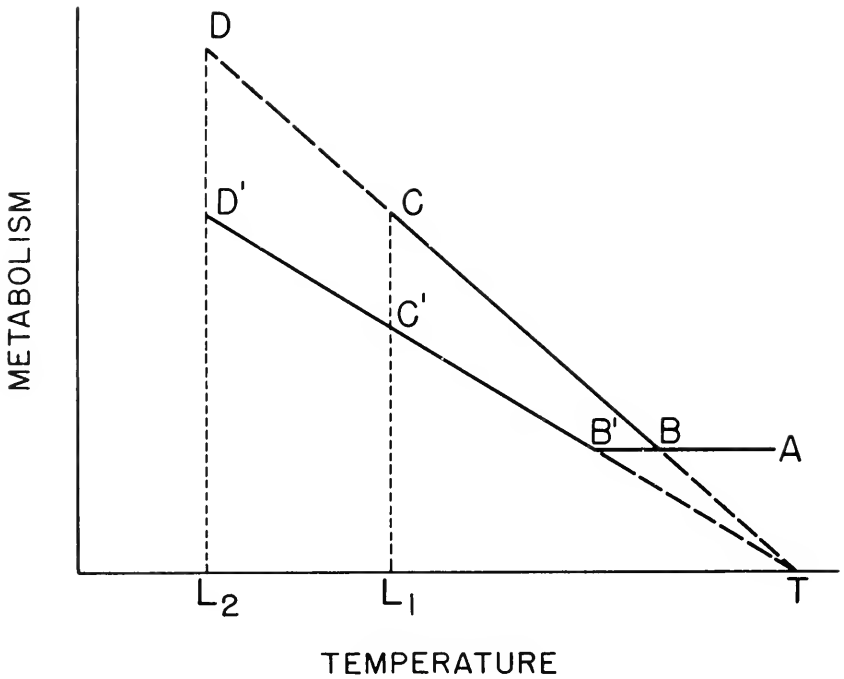


Figure 3. Classical picture of partition of chemical and physical thermoregulation, showing the thermoneutral zone (ABB'), the critical temperature (B, B'), and metabolism slopes (BCD, B'C'D') that extrapolate to body temperature (T). (Hart, 1957).

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insulating ability have been made for several species of birds at thermoneutrality and at a few lower temperatures (Hart, 1957; Misch, 1960; Wallgren, 1954; West, unpublished). Investigations on the Evening Grosbeak (Hesperiphona vespertina) and calculations based on data in the literature indicate that the total insulation (Body T - Air T / (kcal x bird x hour)) increases gradually as temperature falls (Fig. 4). It can be readily observed that the insulation increase is almost linear for some species (Tree Sparrow, Spizella arborea), but a curve for most. The highest temperature at which insulation reaches its maximum is 0° C in both the Cardinal (Richmondia cardinalis) and the Evening Grosbeaks studied by Dawson and Tordoff (1959), while many species continue increasing their insulation to the lowest test temperature (House Sparrow, Passer domesticus, and Variable Seedeater, Sporophila aurita).

Conservation of heat at cold temperatures by peripheral blood flow control and vascular heat exchange in non-insulated portions of the body has been demonstrated in the Glaucous-winged Gull (Larus glaucescens) (Irving and Krog, 1955) and in many other species (Bartholomew and Dawson, 1954; Bartholomew and Cade, 1957; Scholander, 1955).

At air temperatures approaching body temperature, insulation is decreased to its minimum, and mechanisms for dissipation of heat are invoked. These include increase in peripheral blood flow to the legs and feet, increased ventilation, evaporation from the respiratory surfaces, and panting. Some birds are able to increase the temperatures of their legs and feet and still maintain a favorable gradient for heat loss even at temperatures above body temperature (Bartholomew and Dawson, 1958). Birds living in hot regions have evolved behavior patterns enabling them to avoid the heat of day.

Metabolic mechanisms. Thermogenesis in response to cold occurs chiefly by increased physical activity such as exercise, increased muscle tone, and shivering. The heat produced by the specific dynamic action of digestion and assimilation may help to maintain body temperature, but evidence for this is lacking in wild birds (King and Farner, 1961). Non-shivering thermogenesis has been

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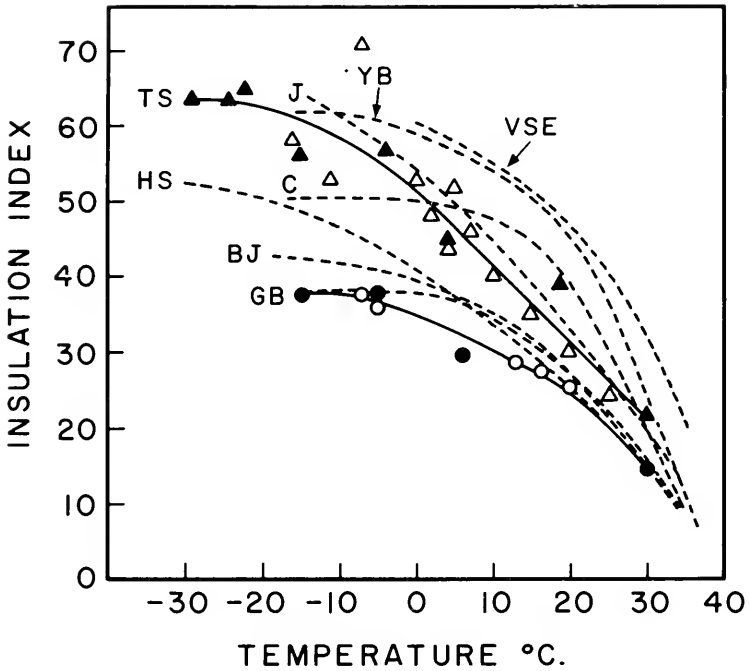


Figure 4. Insulation indices calculated by the formula:

$$\frac{\text{Body } T^{\circ} \text{C} - \text{Air } T^{\circ} \text{C}}{\text{kcal/bird/hour}}$$

Average indices of birds held at constant temperature (●,▲); and of birds under natural fluctuating conditions (○,△). TS=Tree Sparrow (West, 1960), GB=Evening Grosbeak (West and Hart, unpublished). The dashed lines are values calculated from the literature: J=Slate-colored Junco (Seibert, 1949); YB=Yellow Bunting (Wallgren, 1954); VSE=Variable Seedeater (Cox, 1961; C=Cardinal (Dawson, 1958); HS=House Sparrow (Kendeigh, 1949); BJ=Blue Jay (Misch, 1960); GB=Evening Grosbeak (Dawson and Tordoff, 1959).

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described for the white rat (Cottle and Carlson, 1956), but the few experiments done by Hart (in press) indicate that curarized pigeons (Columba livia) are not able to increase their metabolism in the cold.

Recent work by Steen and Enger (1957) on pigeons and by West (unpublished) on Evening Grosbeaks and Common Redpolls indicate that shivering is the major source of heat production by birds in the cold. Experiments on the Evening Grosbeak show that these birds shiver all night out-of-doors at all temperatures below thermoneutrality in both summer and winter. The intensity of shivering increases as the ambient temperature falls (Fig. 5).

Since shivering in particular and metabolic thermoregulation in general are achieved by an increase in energy expenditure, it is pertinent to review some of the recent work on energy exchange in wild birds.

Indirect calorimetric measurements of heat production can be made either by recording the respiratory exchange of oxygen and carbon dioxide or by recording food consumption and excrement production. Although the first method has been widely used by most workers, it is limited in that metabolic rates are sampled over relatively short periods of time. Both "open circuit" and "closed circuit" apparatus have been employed, the latter being further restricted because the ambient temperature must remain constant. Energy balance studies such as those used by Kendeigh (1949), Seibert (1949), Davis (1955), King and Farner (1956), West (1960), and Cox (1961) for wild birds yield an average metabolic level over a period of several days. However, this method is not able to distinguish between metabolic levels at different times of the day.

Automatic recording oxygen and carbon dioxide analyzers have been successfully used to record oxygen consumption and carbon dioxide production simultaneously for 2 to 3 days at a time on wild birds. The birds live in small cages and are supplied with food and drink ad libitum. Daytime and nighttime values can easily be obtained by examining selected portions of the record (Fig. 6). Another advantage of this system is that the birds are not disturbed once the

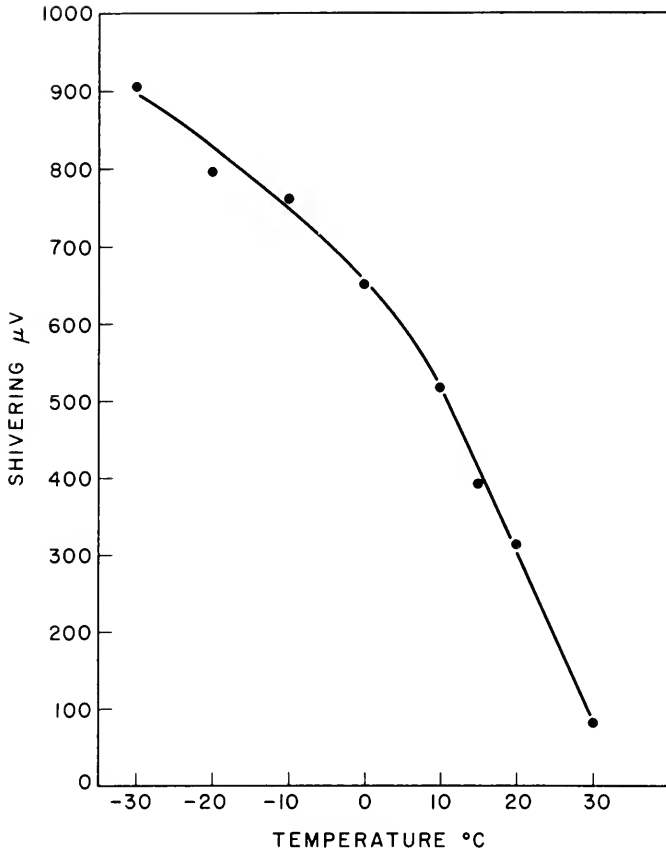


Figure 5. Shivering of summer acclimatized Common Redpolls recorded in microvolts during short term exposure at each temperature. Each point represents averages of four birds.

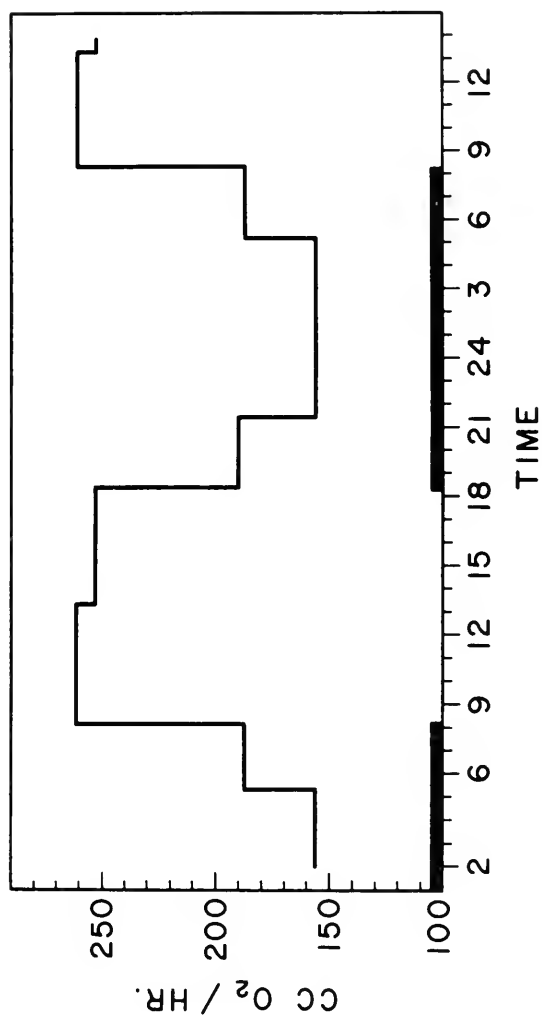


Figure 6. Average diurnal changes in oxygen consumption of eight Evening Grosbeaks recorded for four consecutive days at a constant temperature of 18° C.

experiment is under way. We have observed that metabolic rates remain elevated for about 1 hour after the birds have been placed in a darkened metabolism chamber (West and Hart, unpublished).

Previous thermal history affects the metabolism of an animal at any given test temperature. In order to test the effect of ambient temperature on metabolism, it has been customary to follow one of two methods: (1) Birds are acclimated to a single constant temperature of season and then metabolism values are obtained at a series of test temperatures (Scholander et al., 1950a; Wallgren, 1954; Irving et al., 1955; Steen, 1957; Dawson, 1958; Dawson and Tordoff, 1959; Misch, 1960; Hart, in press; West and Hart, unpublished; and others). (2) Birds are acclimated and their metabolism measured at a single temperature; the temperature is changed and the birds are acclimated and run again, etc. (Kendeigh, 1949, Seibert, 1949; Davis, 1955; Rautenberg, 1957; West, 1960; Cox, 1961; and others).

Many workers have assumed that a linear regression line fitted to the metabolism values at a series of temperatures must extrapolate to body temperature according to Newton's law of cooling (Scholander et al., 1950a; Steen, 1957; and others). This interpretation results in a distinct thermoneutral zone and a critical temperature which divides physical from chemical thermoregulation. Most of the results on small birds obtained by these workers can be equally well interpreted as either a straight line drawn through all points, thus eliminating the critical temperature and thermoneutral zone completely (Fig. 7) or as a curve, which also eliminates the definition of a single critical temperature. The latter interpretation has been suggested by Dawson (1958) for his data on the Cardinal (Fig. 8), and by Dawson and Tordoff (1959) for the Evening Grosbeak.

The slopes obtained by workers measuring metabolism over 24 hour periods are in general much flatter than those obtained in short-term tests on non-acclimated birds. They show no thermoneutral zone, no critical temperature; and the temperature vs. metabolism slope does not extrapolate to body temperature (Fig. 9). Studies in progress on the Evening Grosbeak indicate that the flat slopes may be explained by marked differences in diurnal and nocturnal metabolism and levels of motor activity that change with

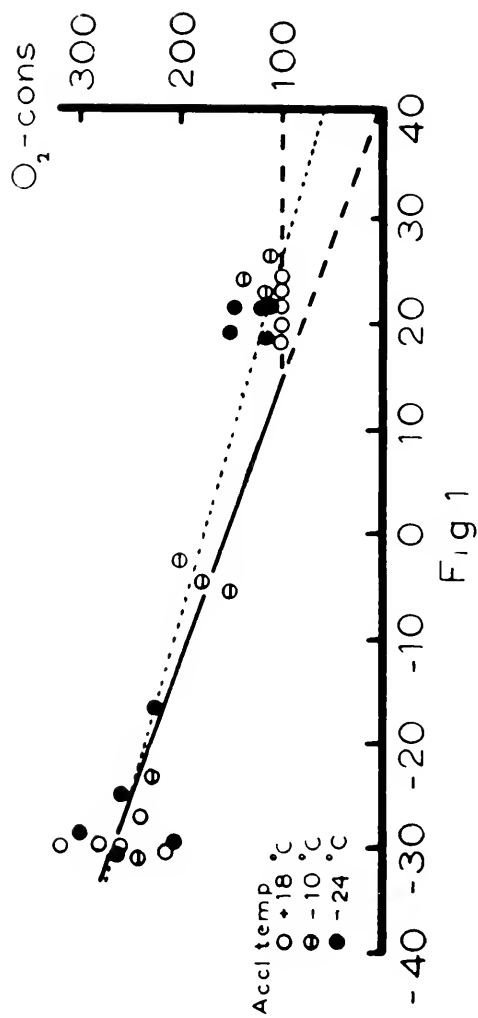


Figure 7. Oxygen consumption of Pigeons at various temperatures. Modified from Steen (1957).

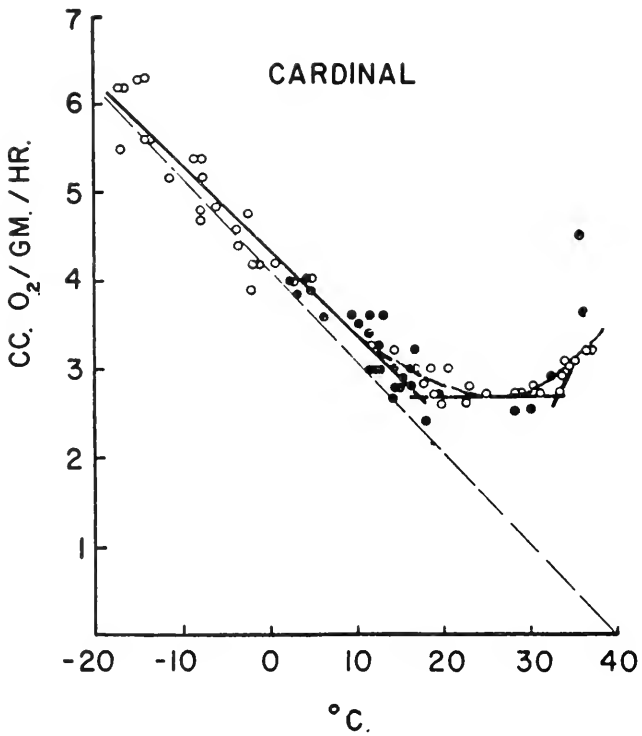


Figure 8. Oxygen consumption of Cardinals at various temperatures. Modified from Dawson (1958). (Courtesy of University of Chicago Press, copyright holder).

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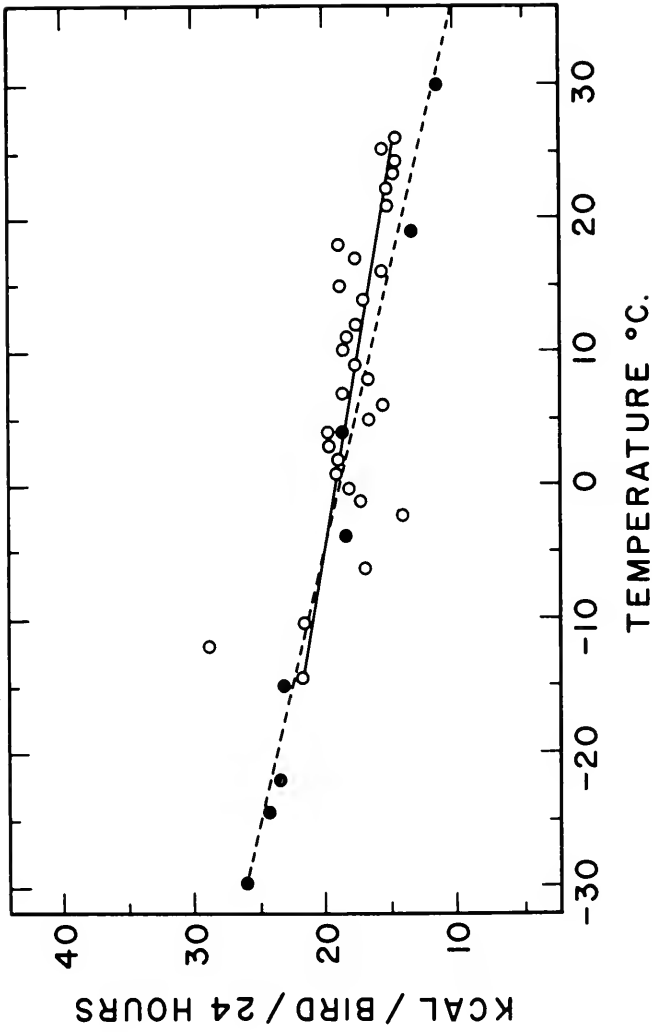


Figure 9. Metabolized energy of Tree Sparrows kept under constant conditions (●), and under naturally fluctuating outdoor conditions (○). Data from West (1958).

ambient temperature (West and Hart, unpublished).

It seems reasonable from the available data that most small wild birds have a curvilinear relationship of metabolism to temperature (Fig. 10). The data in Figure 4 indicate that most birds increase their insulation gradually from high to low temperatures, rapidly at first, then leveling off as maximum insulation is achieved. Heat production, however, increases slowly at first, but then proceeds faster as metabolic mechanisms become the only method of maintaining homeothermy at the lower temperatures. The slope of the curve at the lower temperatures extrapolates to body temperature according to Newton's law of cooling. However, the upper portion of the temperature-metabolism curve extrapolates beyond body temperature since both insulative and metabolic mechanisms are operating simultaneously. Therefore, a prolonged thermoneutral zone and a definite critical temperature probably do not exist for wild birds.

Acclimation and Acclimatization

Gelineo (1955) acclimated birds to three constant temperatures and then obtained metabolism values at a series of test temperatures for each acclimation group. In most cases the cold acclimated birds had a higher metabolism slope and thermoneutral metabolism than the warm acclimated birds (Fig. 11). Similar results have been obtained by Miller (1939) for House Sparrows, Dontcheff and Kayser (1934) and Steen (1957) for the Pigeon, and Wallgren (1954) for the Ortolan (Emberiza hortulana) and Yellow Bunting (Emberiza citrinella).

Contrary to the results obtained with temperature conditioned birds, most species acclimatized to summer and winter seasons do not show differences in their standard metabolisms or in their temperature metabolism slopes (Kendeigh, 1949, and Davis, 1955, for the House Sparrow (Fig. 12); Wallgren, 1954, for the Yellow Bunting; Irving et al., 1955, for the Black Brant (Branta nigricans); Rautenberg, 1957, for the House Sparrow and Brambling (Fringilla montifringilla); Dawson, 1958, for the Cardinal; Hart, in press, for the Pigeon, House Sparrow, Evening Grosbeak, and Starling

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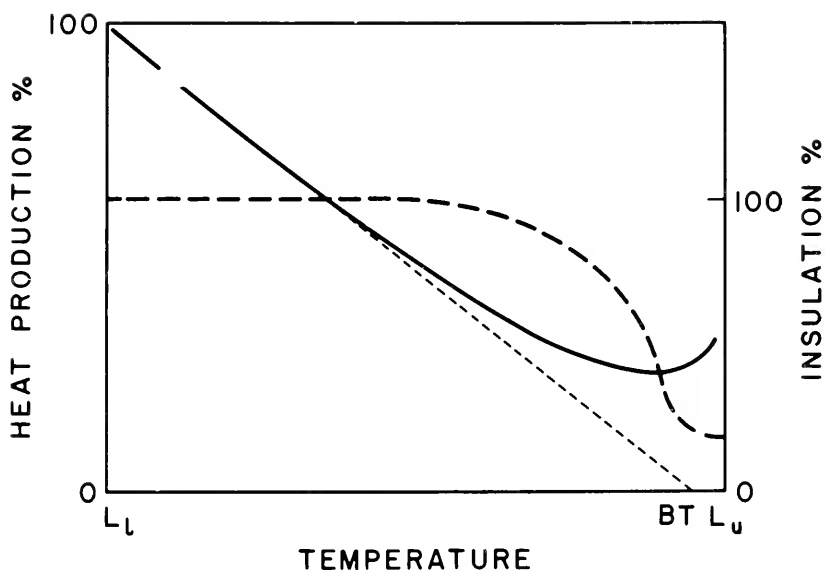


Figure 10. Overlap of insulative (dashed line) and metabolic (solid line) adjustments for thermoregulation in small wild birds. After insulation reaches its maximum, increases in metabolism carry the bird to its lower limit of tolerance (L_l). This slope extrapolates to body temperature (BT) according to Newton's law of cooling. Above body temperature, metabolism increases, and insulation reaches its minimum as the upper limit of tolerance is reached (L_u).

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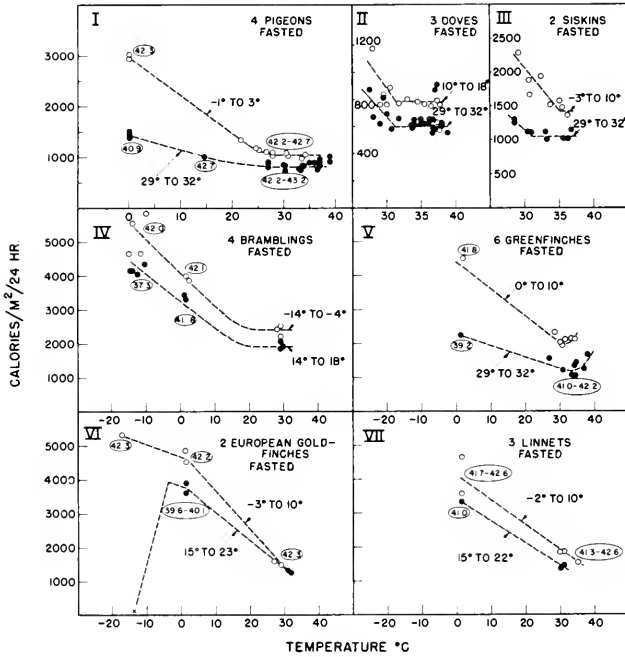


Figure 11. Temperature-metabolism curves of birds acclimated to warm (●) and cold (○). Gelineo's data replotted by Hart (1957).

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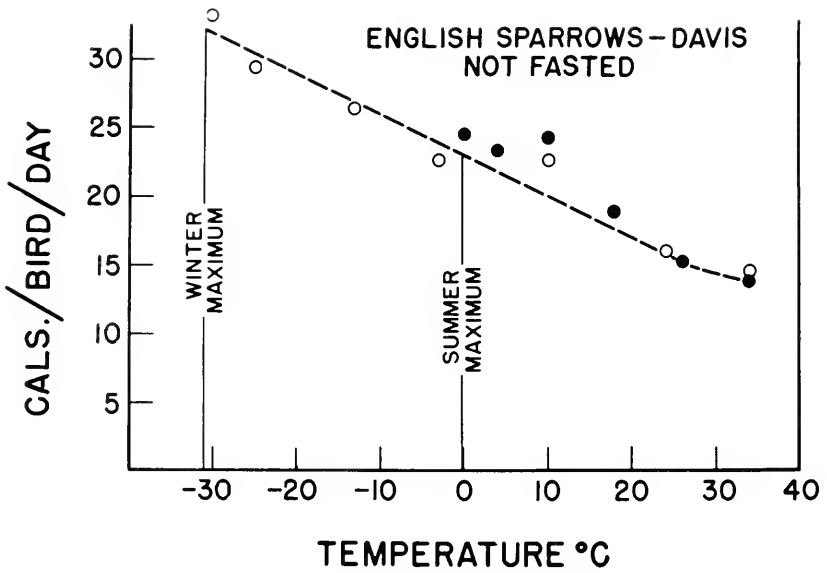


Figure 12. Metabolized energy of winter (O) and summer (●) acclimatized House (English) Sparrows. Davis' data replotted by Hart (1957).

(*Sturnus vulgaris*). The reason for the difference in metabolic response between laboratory acclimated and seasonal acclimatized birds may be that the temperature conditioning process is suppressed by variable ambient temperatures (King and Farner, 1961).

The ability of birds to tolerate low temperature extremes is one of the best indications of seasonal metabolic acclimatization. The work of Kendeigh (1949), Seibert (1949), and Davis (1955) clearly shows that the House Sparrow can extend its low temperature tolerance limit from 0°C in the summer to -31°C in the winter (Fig. 12). In contrast, the Tree Sparrow does not change its lower limit of tolerance and survives to -28°C in both summer and winter (West, 1960). The ability to tolerate low temperatures depends primarily on the length of time that the birds can maintain their maximum metabolic rates. By subjecting seasonally acclimatized birds to a single low temperature, Hart (in press) shows that winter acclimatized Evening Grosbeaks, Starlings, and Pigeons can maintain their maximum metabolic rates for longer periods of time than summer acclimatized birds.

In addition to increased metabolic capacity during the winter, there may be a seasonal shift in insulation since Kendeigh (1934) showed a 29% increase in plumage weights of winter over summer House Sparrows, and West (1960) an increase of 25% of winter over summer plumage weights of Tree Sparrows.

Many species of birds exhibit annual cyclic thyroid activity while others do not (Wilson and Farner, 1960). Wilson and Farner show a direct correlation between thyroid activity and ambient temperature in the Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). These birds experienced an annual temperature cycle of at least 20°C (0°C to 20°C) in eastern Washington. Simultaneously, Oakeson and Lilley (1960) studied the same race of White-crowned Sparrow both on its wintering ground in California and on its breeding ground in Alaska and in contrast, found no annual change in thyroid activity. Wilson and Farner explain this difference by showing that the amplitude of the cycle of temperature that Oakeson and Lilley's birds experienced was probably about 5°C , 15°C less annual variation than their own birds received.

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This brings out an interesting correlation between thyroid activity and metabolic acclimatization in migrant and non-migrant species. From the data cited above and from those of Miller (1939), it may be observed that permanent resident species have pronounced thyroid cycles and therefore greater degrees of metabolic acclimatization because they experience pronounced annual fluctuations in temperature, while migrants, such as the Tree Sparrow or the White-crowned Sparrow studied by Oakeson and Lilley do not have cyclic changes in thyroid activity and therefore little change in metabolic acclimatization because they experience similar temperature conditions in both winter and summer.

Ecological Implications

The physical and metabolic thermoregulatory mechanisms possessed by a species enables it to adapt to a specific set of environmental conditions, i.e., its distribution is limited by these mechanisms. The habitation of any area is determined in part by the ability of a species to acquire not only enough existence energy, but also sufficient productive energy (Kendeigh, 1949) for carrying on energy demanding activities such as molting, reproduction, and migration. In addition to these physiological limits, morphological and behavioral adaptations impose further restrictions on the actual distribution of a species. Although thermoregulatory adaptations to specific environments are covered elsewhere in this symposium, it is important to discuss some of the energy requirements for existence and other activities under natural conditions.

The energy intake of all small wild birds yet studied increases in the winter. The added energy intake is used for existence, which includes maintenance of homeothermy and body weight, acquiring food and drink, the SDA of digestion and assimilation (Kendeigh, 1949), and the deposition of body fat. The added fat may be an emergency measure against severe winter weather or an aid in total insulation. Permanent resident species of temperate regions, such as the House Sparrow, maintain favorable energy conditions throughout the year by increasing their ability to metabolize energy in the cold (see above). Permanent residents of tropical regions, such as the

Variable Seedeater, Yellow-bellied Seedeater (Sporophila nigricollis), Blue-black Grassquit, (Volatinia jacarina), and Green-backed Sparrow (Arremonops conirostris), need vary their energy intake for existence only slightly, with minor changes in temperature and photoperiod throughout the year (Cox, 1960).

Migrant species, however, must adjust to the climatic conditions of two localities. Arctic and temperate breeding birds attain more nearly uniform environmental temperatures by migrating to southern latitudes in the winter. Therefore, the lack of metabolic acclimatization in the Tree Sparrow (see above) may be a result of spending the whole year in a relatively constant climate.

In contrast to permanent resident species, migrant birds must increase their energy intake for migratory flights in the spring and fall (Farner, 1955; Rautenberg, 1957; Kendeigh et al., 1960). The added energy intake is used for the deposition of migratory fat, and in caged birds, for motor activity at night (Zugunruhe). When fat stores are completed and weather conditions are satisfactory, actual flight, utilizing the stored fat, occurs. The pattern of added energy intake for fat deposition alternated with migratory flights is repeated until the final destination is reached (Wolfson, 1954). The added cost of fat deposition and spring nocturnal unrest increases the daily energy intake of White-crowned Sparrows by 30% to 50% (King and Farner, 1956) and the intake of Tree Sparrows by 21% to 22% (West, 1960; Kendeigh et al., 1960).

Following migration, reproductive activities are initiated. The amount of energy required to produce a clutch of eggs is undoubtedly considerable although it has not been experimentally determined for wild birds (Kendeigh, 1941). The added cost of incubation of eggs by the female Tree Sparrow has been calculated to add about 22% to its existence energy requirement per day (West, 1960). Kendeigh (1961b) shows that incubating House Wrens (Troglodytes aedon) also require 23% more energy while incubating.

Most small passerines have a complete post nuptial molt in the fall. The growth of new feathers requires energy. Metabolic rates of the Chaffinch (Fringilla coelebs) (Koch and deBont, 1944)

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Yellow Buntings and Ortolans (Wallgren, 1954) increased 10% to 26% during molting. The increases, however, are variable, and it appears that the greatest energy cost occurs during growth of the large flight feathers of the wing and tail (Koch and deBont, 1944). It is doubtful that the gradual loss and replacement of feathers causes a measureable lowering of body insulation in most passerines, and any metabolic increase, therefore, is due to the production of new feathers (King and Farmer, 1961).

Davis (1955) did not find an increase in metabolized energy of House Sparrows during molting, although his data exhibited greater variability at this time. King and Farmer (1961) have pointed out that the added daily cost of producing new feathers is so small that it might not be detected in food consumption experiments. West (1960), however, found a 27% increase in metabolized energy of molting Tree Sparrows for over one week. This may have been during the time of flight feather regeneration and an average value over several weeks might be lower.

When the values for fat deposition, migration, reproduction, and molting are added to the daily existence level, the total energy expenditure of a single species can be traced throughout the year (Fig. 13). The added cost of living a free existence as opposed to a caged existence may be greater in the winter than in the summer due to the difficulty of finding food. The uniform spacing of energy demanding activities is such that the average daily intake of energy is about the same throughout the year.

A species must be confined to localities where it can secure enough energy not only for existence, but also for all its essential activities. Therefore, climate, and particularly temperature, plays a major role in controlling distribution by excluding species from regions which impose energy requirements exceeding metabolic capabilities.

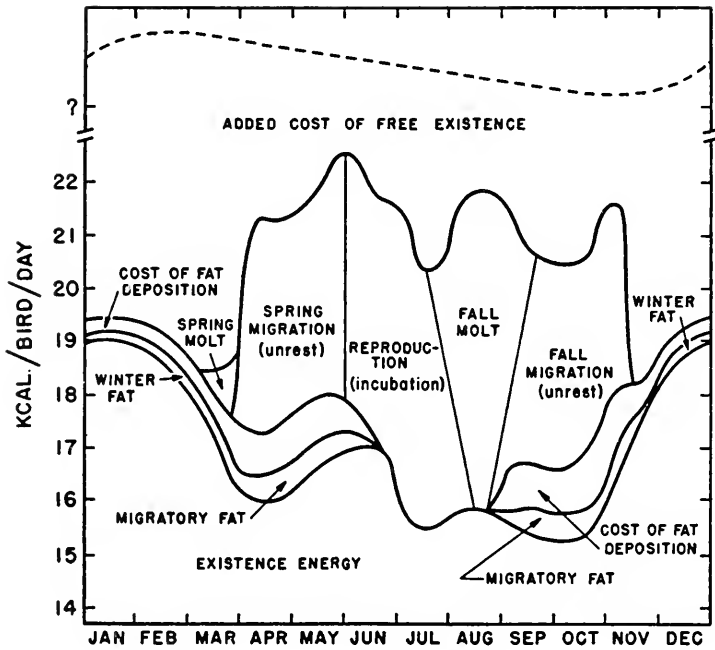


Figure 13. Total energy requirements of Tree Sparrows throughout the year. The lowest curve is that of existence energy to which the energy required by various activities has been added (West, 1960).

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SUMMARY

Birds maintain relatively constant body temperatures by regulating mechanisms for heat production and heat loss over a wide range of environmental temperatures.

The variable insulative ability of the plumage is the chief mechanism for prevention of heat loss. As temperature falls, insulation gradually increases until it reaches a maximum. At the same time, peripheral circulation decreases and heat is retained in the core of the body. Simultaneous with the increase in insulation, shivering increases as the ambient temperature drops. After the insulation reaches its maximum, metabolic mechanisms alone maintain homeothermy until the lower limit of temperature tolerance is reached. In most small passerines, the total effect of combined insulation and shivering responses to temperature results in a curvilinear relationship of metabolism to temperature, with no prolonged thermoneutral zone indicated.

Birds acclimated to low constant temperatures in the laboratory generally have higher metabolic rates at any temperature than those acclimated to warm temperatures. Birds acclimatized to different seasons, however, show little change in metabolic response at thermoneutral temperatures. Seasonal changes in thermoregulatory mechanisms involve an increased ability to produce heat by increasing the metabolic rate in the cold of winter for extended periods of time and possibly an increase in the amount of plumage insulation.

Existence energy requirements of small wild birds living in temperate regions are increased in the winter. Permanent residents may have a more pronounced seasonal difference in their ability to tolerate low temperatures than migrant species since they encounter greater extremes of temperature.

The added daily cost of nocturnal unrest and of depositing migratory fat differs slightly among migrant birds according to the length of time spent in premigratory preparation and in the average

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length of each migratory flight. The average daily intake of small birds probably remains relatively constant throughout the year, since energy demanding activities such as existence in winter cold, deposition of fat, migration, reproduction, and molting are uniformly spaced. The distribution of a species is therefore limited to locations where the climate permits fulfillment of all essential energy demanding activities.

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WEST

DISCUSSION

JOHANSEN: I am very impressed with all the facts that are available on birds now. I think this surpasses what we know about mammals, particularly with regard to ecological factors involved in temperature regulation. I was particularly pleased to hear your doubts as to whether we really can consider the critical temperature as a fixed point, and also whether insulation is gradually mobilized during the period of active increase in metabolism. As I pointed out in my paper, I think this applies also to the more primitive mammals.

WEST: And I think also to the small mammals.

JOHANSEN: Definitely. I had another question, and that is, how does this ten-fold difference in electrical activity correspond with the actual metabolic difference between the two? Could you comment on that?

WEST: We do not have the metabolism of the rats worked out in calories. Also no simultaneous measurements of metabolism and shivering have been done at a series of temperatures for mammals.

JOHANSEN: I was wondering whether you could correspond metabolism with electrical activity.

WEST: I have done it for birds but not for mammals. In birds there is a linear relationship between electrical activity and metabolism. The slope varies with the size of the bird. So far we have plotted data for three species and the smallest, the common redpoll, increases its electrical activity much faster than it does its metabolism. The larger birds do not increase their shivering as fast and there is about a 45° slope for birds of about 100 grams.

HART: It is much higher for birds than it is for mammals.

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HART: No, not ten times. For example, the pigeon has about the same weight as the rat, and it has about five times the electrical activity. We do not know enough about different species of birds, but this is the trend. It seems there is a much greater electrical activity in birds.

WEST: I think this will work out better when we put it on a power spectrum basis rather than a simple muscle potential.

HANNON: It would seem, if you had a good measure of shivering activity, you should be able to have a 45° relationship between metabolic change and shivering change or muscle activity change.

WEST: Yes, muscle is the source of total heat production and I believe that if the results are standardized on a body surface basis the lines would be close together.

HANNON: Because your peak microvolts went up considerably faster than your metabolism did.

HART: Yes, that went up about ten times.

HANNON: For 100% increase in metabolism, there is a considerably greater increase in peak microvolts as a measure of your shivering.

WEST: I agree, for the smaller species.

PROSSER: After all, what you are concerned with is the energy produced by the chemical reactions in the muscle. Might not a delicate vibration detector or something for measuring movement be as effective? Have you tried any of these spring gadgets?

IRVING: Ballistic cardiograph?

PROSSER: Yes, like a ballistic cardiograph.

WEST: We have not tried any, no.

WEST

ADAMS: I would suggest that there must be a constant difference in the relationship between the shivering index as you have it and the oxygen consumption, since you do have a straight line relationship. And if this is true, then perhaps we have a frequency recording artifact all the way along the scale, not just at one peak.

WEST: The frequency of shivering is very low at the higher temperatures and we do record that faithfully, because it only goes up to around 200 cycles per second or so, but our recent analysis shows that intense shivering goes as high as 700 c.p.s.

PROSSER: Of course you have to sacrifice the bird, but just as a check it might be useful to do phosphocreatine breakdown. I would like to ask one question about the fact that you find no difference in the slope or in the shivering response with the seasons, but do find that the winter birds can maintain their metabolism longer under cold stress. Now, this suggests that acclimatization may be an endocrine phenomenon. Have you any information about the state of the adrenal cortex?

WEST: Not about the adrenal cortex, but a little on the thyroid. But Wilson and Farner, and Oaksen and Lillie have found that the thyroids of permanent resident birds that were held in one spot increased in the winter time because the temperature fluctuated greatly, which corresponds to the permanent resident metabolic acclimatization. But birds studied on their wintering ground in California and on their summer ground in Alaska, showed no difference in thyroid, "because" they experienced a temperature fluctuation both summer and winter of 5°C , whereas those maintained in Washington had a temperature fluctuation of 20°C . This may be a tie-up there, although this is very tenuous, and there are results in thyroid activity going in the other direction for some species. I do not know anything about the adrenal.

IRVING: I look at migratory birds from the wrong end. I mean from the unconventional end of being on the arctic ground where the birds arrive after migration, instead of in the temperate places from which they are preparing to start. It has always been

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interesting for me to see this migratory fat still preserved by birds at the time of their arrival on the nesting ground, and then diminishing markedly during the period of courtship of the male and somewhere along during the incubating period of the female. So I am not sure that it is strictly and seasonally a migratory fat, although it may be useful for the bird to pack his California fat up to Alaska. But certainly the moment when migratory fat is utilized is, like the fat of the bull fur seal, during the actual breeding period.

WEST: Are you speaking of shore birds primarily?

IRVING: It is pretty general among the birds arriving in arctic Alaska breeding grounds. There are some 40 species for which I have sufficient records to be indicative including all families and sizes.

WEST: Do you think possibly a sandpiper or plover who may fly non-stop over a great distance could retain a large proportion of his fat when he reaches the breeding ground?

IRVING: They do have considerable fat when they arrive so far as I can compare weights with those of similar birds when they were ready to depart from the wintering grounds. They may be a little less fat, but they are still very fat birds.

WEST: The question then arises how they get enough energy to fly that distance unless they stop enroute to keep augmenting their fat stores, which we know to be the case in passerines.

IRVING: I realize these are net results, but the situation of the observer can change one's point of view. You mentioned the energy requisite for reproduction. The other day I was looking at the eggs of Least Sandpipers, which, like all sandpipers, are quite large. We weighed these and the four eggs weighed 25 grams. They were laid on four successive days and the female bird which produced them weighed 21 grams; I suggest that you might start introduction of Least Sandpiper blood into white leghorns because the sandpiper equals her weight in egg production in four days, instead of the two months necessary for the good white leghorn to equal her weight of egg production.

WEST

FOLK: I have two points to make: one is, we are equally surprised to find a large quantity of fat in hibernating ground squirrels after 4 months of hibernation. Not all animals, but some are very conspicuously fat in spite of the fact that they awaken periodically. This matches Dr. Irving's observations on birds. The second question is a technical one. In measuring the oxygen consumption of the evening grosbeaks you described a 3-day run with a hood on the cage. Do you continue a photo-period during this period?

WEST: Yes.

FOLK: And what is the photo-period?

WEST: Ten hours of light. We use a lucite cover with a loose polyvinyl plastic cylinder taped to it that slides down over the cylindrical cage and is sealed to the sides of the cage with electrical tape. An outlet is provided at the top where air is pumped out into the oxygen analyzer. An inlet is provided at the base of the cage. These cages are identical with the cages we use for acclimation or for housing the birds, and so we just have to drop the hood over them. I think there is a lot to this psychological business. They do not have to adjust to a new cage.

IRVING: I have seen calculations on fat and tried to make some myself to indicate that a gram of fat will transport a 20 gram bird quite a long distance; the several grams that they have is adequate for quite a considerable extra expenditure of metabolic energy, but how about the requirement for water? I have not seen reference to any visible reserve for water.

WEST: You mean birds migrating over the ocean?

IRVING: Yes. I wonder how they hold out.

WEST: You do not think they get enough metabolic water?

IRVING: I do not know. Can you calculate the water requirements and relate them to stores?

WEST: I have not done so.

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IRVING: Rough calculations which I have tried to make and which I do not trust suggest that water may be much more critical than the fat.

WEST: You are thinking, of course, of birds that are flying over the ocean.

IRVING: Yes.

WEST: And I am always thinking of sparrows that hop, skip, and jump 100 miles a flight and then come down.

IRVING: This flight is nothing to them; it takes an hour or two.

WEST: Yes, they do about 30 miles an hour, roughly. How long does it take for an Arctic Tern or Golden Plover to go its distance non-stop? Do they not go very fast?

IRVING: The travel of the plover from Alaska to Hawaii and from New Foundland or Nova Scotia to South America is a couple thousand miles non-stop.

WEST: How many hours, forty-eight hours?

IRVING: It is in the order of a couple of days rather than so many hours.

WEST: I think they could probably make it all right with respect to water requirements.

PROSSER: Are you sure they never put down?

IRVING: It has not been observed and it is inconceivable that they could derive any benefit from it except to sit out the time. They are not swimming birds. They could not feed there.

HART: Could they drink the sea water and excrete the salt?

WEST

MORRISON: I would like to return to the matter of the applicability of these simple relations between metabolism and ambient temperature, which was first raised by Dr. Johansen's talk. I do not think that we should speak as though this relation is discredited and not applicable in these animals. We must remember that these represent limits which any animal will follow more or less closely. They are limits of minimum metabolism and of minimum thermal conductance and as such are excellent descriptive terms. Now, the great deviation of your birds from the limiting curve is very interesting as representing a physiological inefficiency since this extra metabolism need not be expended if the bird were using the maximum potential of its insulation. It would be useful to describe the bird both in terms of its limiting conductance, and also in terms of its deviation from that limit. Perhaps this might be in terms of the temperature range over which it deviates and the ratio of the measured and the basal metabolism at the critical temperature.

WEST: I agree to that, but with these birds there is such great deviation we should not force our data to fit the classical theory, just because it is a classical theory.

JOHANSEN: Critical temperature as a term is only meaningful when we know that the core temperature stays constant up to this point.

MORRISON: I am not sure that the critical temperature has been strictly defined in terms of these refinements.

PROSSER: Why does a bird molt? It seems to me a most wasteful thing. What is the advantage of getting rid of an old set of feathers to grow a new set?

WEST: They wear out.

PROSSER: Are new feathers really better insulators?

WEST: They probably are. I do not know, but they wear out. From the behavioral standpoint, they have to grow their new colors again for the fall and spring. We know that the total weight changes,

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but we do not see any evidence in any of our curves that there is any effective increased insulation.

HANNON: This goes on in most animals, does it not? We grow more skin continuously.

IRVING: If you look at the plumage of birds from tropic or arctic locations, you have a hard time convincing yourself by that examination that one is arctic and one is tropic. Among the jays you might think that there is a little thinner body plumage on the tropical than on the arctic form, but the quantity of feathers does not seem to vary very much with the climate where the specimen originated. Of course feathers are not for insulation alone; they serve an aerodynamic function in which the dimensions of a bird that would be affected by increasing its feathers would quite destroy its aerodynamic qualities, although a mammal can carry fur ten times as long if he does not trip over it.

PITELKA: Your question, Dr. Prosser, is aggravated by a circumstance which is not yet well documented in the literature, which is that some tropical species, if they are not breeding, are molting. Dr. Irving a moment ago mentioned tropical jays; I have some data shortly to be published for a 50-gram species of tropical jay. The breeding season is March through June or July and otherwise the population as a whole is molting, starting its molt in late May and continuing into February, so that in effect the birds are either breeding or molting. And when we get situations like this, contrasting with tree sparrows or longspurs which molt in a very short time, then the whole business of budgeting of energy and the advantage of the molt is so delicately adjusted as it is, becomes more interesting and intriguing.

I would like to comment on a couple of other things about plumage which are relevant to Dr. West's remarks about insulative problems and also relevant to something Dr. Irving said a moment ago. There is one kind of difference between high latitude and tropical birds which, to the best of my knowledge, has gone unnoticed in the literature, and which as you will see, must obviously bear a great deal on the capacities of birds that deal with low temperatures

WEST

and also bear a great deal on the rates at which they can or do adjust to lowering temperatures. We talk about feather tracts, and apteria, but I invite you to trap a Snow Bunting in late May and rip all its contour feathers off. In other words, rip the feathers off the pterylae, that is, the feather tracts. What will you have left? You will have a body which is covered with a dense down which covers the apteria.

I have prepared finches from high latitudes and low latitudes, and there is a striking trend. The lower latitude finches are genuinely naked on their apteria, but the high latitude ones which I have examined, the Golden Crowned Sparrow, the Lapland Longspur, and the Snow Bunting, are not. This must be a relevant consideration to those interspecific differences on Dr. West's graphs which seem puzzling.

Another little detail which is perhaps a little more esoteric is this: in larger passerines like the Steller's Jay, there is a highly modified, stiff, hair-like feather, which is distributed over the body. What is this for? I am not sure that I have an answer to what it is for, and I have not said anything about this in print because there is such a depressingly large European literature on plumage that I have not gone through it yet to see if somebody has said something on the matter. But these stiff, hair-like feathers, distributed over the body on a large passerine which has a very lax and dense plumage, could increase the efficiency of spacing of the plumage when the bird expands it and contracts it; and the presence or absence of these hair-like feathers must be another little detail that has to be plugged into these considerations of why Dr. West's curves deviate as they do.

WEST: What is the distribution of those? Are these filoplumes?

PITELKA: Yes, filoplumes. They are regularly distributed among the contour feathers.

WEST: How about on the smaller birds, sparrows?

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PITELKA: I do not think they are present. I am not sure about that. I have not looked for them, actually. If they are there at all, they are certainly not easily noticed.

HUDSON: I would like to add to Dr. Johansen's, Dr. Morrison's, and Dr. West's remarks with respect to the lower critical temperature. In our laboratory we have had a number of cases in which we have been unable to get nice extrapolations of the metabolic rate to the appropriate body temperature, and in some cases we get extrapolated body temperatures as high as 44°C and 45°C . At the same time, using the same techniques and animals from similar areas, we are also able to successfully extrapolate, so that we are reasonably certain that it is not our technique, but have the feeling that possibly there was some change in conductance going on even below the lower critical temperature.

PROSSER: May I ask just one more question about the computed insulation curve? If similar curves are constructed for mammals, what would be the shape and the value of the index that Dr. West presented?

HART: In lemmings, during activity there is a large variation, but during rest in mice at least, the variation of insulation with temperature was similar to the hypothetical insulation curve for birds except that it conforms more closely to the critical temperature. In other words, the curve becomes flat at higher temperatures. If body temperature is constant and the correlation between metabolism and temperature extrapolates to zero at a value higher than body temperature, then insulation would increase with fall in temperature in a manner comparable to that seen in birds.

HUDSON: And these are also animals which have, from general appearance, reasonably good coats, have metabolic rates that are approximately what you would expect from their body size, but also have lower critical temperatures that are extremely high, that is above 30°C . So that on the basis of general judgment you would expect the animal to have the capacity to continue his regulation by physical means through much lower temperatures than he does.

WEST

IRVING: It is so hard to figure on some of these things in examining the metabolism of the Brant in summer and winter. The Brant is a big bird weighing a kilogram and a half, and with feathers so thick that when you grasp hold of him you cannot feel through the underlying bird or meat, and yet its metabolic rate begins to increase at just about freezing temperature. It is a bird with the thickest insulating feather cover that you can find, and yet he does not use it for insulation. Of course the Brant, like the other water fowl, follow the open water throughout the year and perhaps they do not need any more insulation, but that does not give any physical explanation. In fact, the explanation is probably physiological rather than a matter of simple feather thickness.

MORRISON: As far as changing body temperature goes, of course this relation is related to difference between body temperature and ambient temperature.

IRVING: Are you not working in a limited range of animal size where the measurements are difficult? Perhaps life itself is difficult for animals of these very small dimensions and they have to resort to metabolic subterfuges which are legitimate for them but illegitimate from our point of view. They are difficult to examine because you are looking at the 10 to 100 gram or so size range. Perhaps some clarification would come if you went to larger birds; I think your only representative above 100 grams was the pigeon, was it not?

WEST: Yes, I was concerned with the small wild birds, most of the passerine group.

PROSSER: Are you saying that this temperature-metabolism curve rises continuously as you go to lower temperatures, and that you have no thermo-neutral zone or critical temperature for smaller birds, while in a larger bird there is a critical temperature?

WEST: Yes.

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IRVING: I do not say that these deviations from what we expect to be the rule, or what we would like to hope would be a rule, are incorrect. I am sure they are correct, but they may represent the deviations of birds on account of size, as small mammals deviate.

RACIAL VARIATIONS IN HUMAN RESPONSE TO LOW TEMPERATURE

Frederick A. Milan

The investigations of racial variations in thermoregulation have been based on the premise that races of mankind inhabiting regions characterized by seasonal or diurnal periods of low temperature are biologically adapted* to life in these environments. It has been assumed that thermoregulation in a race living in regions of low temperature may function differently from that of a race in a warmer climate. These studies of racial variation in physiologic function are attempting to accomplish the task recommended for biologists by Prosser (1959). This task is to assess critically the functional adaptive features (including behavior) that can describe the unique fitness of a species to its environment.

According to the inferential evidence of archaeology and paleontology, Homo sapiens evolved in tropical Africa and Eurasia, and his original geographical distribution resembled that of the present day Old World non-human primates. Early hominids presumably lived in a thermally neutral environment. It has also been clearly shown by finds in Tanganyika that prehomnids had already acquired tools and fire before Homo sapiens evolved as a species (Washburn, 1959).

It is obvious that man erects a cultural screen of dwellings, clothing, living techniques, and behavioral adjustments between himself and his environment. Except at high altitudes (as on the Bolivian altiplano, for example) where little can be done about low oxygen tension by preliterate peoples, man's cultural screen effectively ameliorates environmental stress and is an essential part of his external temperature regulation. This cultural carapace must be considered in enumerating human groups chronically exposed to low temperatures.

*A biological adaptation is "...an aspect of the organism that promotes its general welfare, or the welfare of the species to which it belongs in the environment it usually inhabits" (Simpson et al., 1957).

MILAN

Experimental data are available which describe some aspect of thermoregulation in peoples as various as Eskimos, Arctic Athapascans, South American Indians (the Alacaluf), Norwegian Lapps, Australian aborigines, African Bushmen, American Negroes, European Norwegians, and a host of North American White controls. In this paper these data will be reviewed and the results of my own experiment which was designed to further investigate thermoregulation and to compare tissue insulation in Anaktuvuk Eskimos, Athapascans, and Caucasian soldiers will be presented.

A HISTORICAL REVIEW AND LITERATURE SURVEY

The Eskimo

Possibly because of their geographical location, the earliest studies were undertaken on the Eskimos. The Eskimos are a genetically, linguistically, and culturally homogeneous population living along the coasts of Greenland, Northern North America, and a small area of Siberia. It is apparent that they have been in the Arctic for a considerable length of time. The Denbigh Flint Complex of Norton Sound, presently the oldest cultural assemblage on the Alaskan side of the Bering Strait, has been dated at between 2500 and 3000 B. C. Eskimo type cultures have succeeded one another in this area from about 500 B. C. to the present (Giddings, 1960). Material from the bottom layers of a midden at Nikolski, Umnak Island, in the Aleutians has been dated at about 3000 B. C. (Laughlin and Marsh, 1951).

A folk migration of expert arctic travelers, carriers of the Thule culture, wandered from the Bering Strait 6,000 miles to Greenland about 1,000 years ago and caused the present linguistic, racial, and cultural homogeneity over this vast area (Collins, 1954). The Thule people replaced the earlier arrivals, the Dorset people, who had been in the eastern Canadian Arctic and Greenland since about 675 B. C. (Larsen and Meldgaard, 1958). The first European-

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Eskimo contact occurred in 988 A. D. when Eric the Red encountered the Greenlanders.

The main characteristics of the climate of the high Arctic are year-round aridity, low temperatures and high winds with drifting snow in winter and cool temperatures and a high incidence of fog in summer. It has been clearly recognized by physiologists that the success of the Eskimo in exploiting his environment is due to the fact that he carries his private microclimate about with him. Nevertheless, it is difficult to understand how one could live in the Arctic and not suffer occasional cold exposure, and therefore many physiological investigations have been designed to elucidate the more subtle differences in thermoregulation.

Basal metabolism. August and Marie Krogh (1913) reported that the Greenland Eskimos were utilizing more than 300 gm of protein in their diets per day and later suggested to Hygaard (1941) that the elevated heat production (+13% of the DuBois Standard) of 22 Angmagssalik Eskimos of East Greenland may have been due to dietary factors. An elevated basal metabolic rate has been reported by almost all investigators of the Eskimo. Rodahl (1952), who has reviewed the early literature, measured surface areas, and measured the BMR's of 73 healthy Eskimos, concludes that apprehension and the high protein diet are the reasons for the high BMR. MacHattie et al. (1960), however, on the basis of the 24 hour metabolic studies of the night fuel energy fractions in Anaktuvuk Pass Eskimos, consider factors (unknown at present) other than the SDA of protein to be involved.

It is puzzling to many that the SDA of protein has such long lasting post prandial effects on Eskimo metabolism. Keeton et al. (1946), however, fed experimental diets high in either protein or carbohydrate to 12 male conscientious objectors for 5.5 months and reported an 18% to 19% increase in metabolism (6 hours after the last meal) due to the SDA of protein. And Hicks et al. (1934) reported the SDA of raw meat ingested by Australian aboriginals to be 80% after five hours.

Brown et al. (1953) measured BMR's in nine males and seven females at Southampton Island and reported them to be between 124% and 130% of normal. They described their subjects as clinically hypermetabolic but not hyperthyroid in the sense of thyrotoxic. The suggestions of others that the elevated BMR might be due to anemia, polycythemia, racial characteristics, unidentified disease, or the high protein diet were discussed. They have concluded that the high metabolic rate was not entirely the result of a high protein diet, but that the diet is merely another manifestation of the effects of the environment and the food available.

Thyroid metabolism. Gottschalk et al. (1952) measured the protein bound iodine in seven U. S. soldiers attending an arctic indoctrination course at Fort Churchill, seven male Eskimos from Southampton Island, and seven Eskimos from Chesterfield Inlet in winter. There was no change in the soldiers' basal metabolic rate or PBI due to their arctic sojourn. The Eskimos had significantly higher values in PBI (4.2 to 9.0 microgram percent) than euthyroid patients in U. S. hospitals.

Rodahl et al. (1956, 1957) administered tracer doses of I^{131} to 84 Alaskan coastal and inland Eskimos, 17 Athapascan Indians of Ft. Yukon and Arctic Village, and 19 white controls to assess the role of thyroid in man during cold exposure. Except for the inland natives, there was no significant difference in thyroid uptake or urinary elimination of I^{131} or in PBI 131 and no seasonal difference in PBI. There was no significant difference between natives and whites in PBI. The Anaktuvuk Eskimos and the Arctic Village Indians had high and rapid uptakes of I^{131} which were related to the low iodine in their diets and to the high incidence of endemic goiter. A reduction in the rate of uptake of I^{131} occurred following supplementation daily for 3 months of 0.6 mg potassium iodide.

Blood volumes. Brown et al. (1953) measured blood volumes by dilution of Evans Blue dye and hematocrits in 22 male Eskimos at Southampton Island. They reported blood volumes to be 124% to 142%

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above normal (normal is 100%). The increase was noted in both the plasma and in the total red blood cell volume.

Response to extremity cooling. Pecora (1948) studied the "pressor response" in 23 male Eskimos of Nome and Fairbanks using a sphygmomanometer and compared the results with those of similar experiments conducted on 44 Caucasian soldier controls. An arm was immersed in unstirred water with a temperature of 4°C to 5°C . The Eskimo group had a higher basal blood pressure, but the increase due to the cold immersion was less than in the control group. In addition, the Eskimos reported less subjective pain.

Brown et al. (1952), by venous occlusion plethysmography, measured hand blood flow in 22 male Southampton Island Eskimos and 37 Queens University medical students in room air and in water baths ranging between 5°C and 45°C . The hand blood flow of the Eskimos was nearly twice as great as that of the Caucasians in room air of 20°C . Values were: Eskimos, 8.6 cc/100 cc tissue/min; controls, 4.7 cc/100 cc tissue/min. The Eskimo hand flow was greater at any given water bath temperature.

Brown et al. (1953), by venous occlusion plethysmography, determined forearm blood flow and measured the temperatures of forearm skin, subcutaneous tissue, muscle, and rectums of 29 male Southampton Island Eskimos who were not all racially pure and 37 male Kingston Ontario medical students. In a 45°C water bath, the blood flow was similar in both groups. Below 45°C the Eskimo group had a greater blood flow. In water baths below 38°C the Eskimo forearm muscle temperature was lower as a result of a greater venous return and consequent cooling of arterial blood. In the 5°C bath, the Eskimo forearm flow was 3.8 cc/100 cc tissue/min in contrast to 1.5 cc/100 cc tissue/min in the medical students.

Page et al. (1953) investigated hand blood flow, subcutaneous temperatures, muscle temperatures, and rectal temperatures in Southampton Island Eskimos and a control group of medical students during heating and cooling of the legs in water baths. During heating at 42.5°C forearm muscle temperature and blood flow was

greater in the control group. During cooling of the legs at 10°C the Eskimos showed little change in blood flow in contrast to the controls who showed a pronounced fall.

Elsner (1960) measured limb blood flow in six Anaktuvuk Eskimo males and athletic and non-athletic Caucasians. Limb blood flow was somewhat elevated at rest in the Eskimos.

Meehan (1955) measured the temperature at the base of the nail of the right index fingers of hands immersed for 30 minutes in stirred ice water in 52 Alaskan natives (14 from Barter Island, 24 from Fort Yukon, and 14 from Gambell), 38 American Negroes, and 168 Caucasians. During the last 25 minutes, the Alaskan natives maintained the highest mean finger temperatures. Only 5% of the Alaskan natives, in contrast to 21% of the Caucasians and 62% of the Negroes, had mean finger temperatures of 0°C during the last 25 minutes.

Pain sensation. Meehan et al. (1954) investigated the "warm" pain threshold in 26 Athapascan Indians, 37 Anaktuvuk Pass Eskimos, and 28 white controls. A 3-second thermal stimulation on the back of the hand was used. The threshold was about 43.1°C to 43.7°C , and there was no significant difference between the groups.

Differential sweat rates. Rodahl et al. (1957) investigated the comparative sweat rates of six male Anaktuvuk Pass Eskimos and five male Caucasian controls exposed nude for 3 hours to several ambient temperatures during exercise (15 minutes at 3.5 mph on an 8.6% grade) and during a 3 hour walk wearing standard clothing at -23°C . They found that at all ambient temperatures the resting metabolic rate for the Eskimos exceeded that of the Caucasian group by over 30%. The average skin temperature of the Eskimo tended to be higher at all environmental temperatures below 35°C . The Eskimo skin, particularly of the forehead and back, had a greater concentration of active sweat glands at 33°C environmental temperature. During the treadmill exercise the group differences were not significant, although the Eskimo group had to dissipate 21% more heat to maintain the same body temperature. According to nude

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weight loss, the Eskimos' sweat rate was twice as great during the 3 hour walk at -23°C . The elevated metabolism of the Eskimo required that they increase total body heat loss to maintain thermal equilibrium, and the sweating mechanism accounted for the dissipation of 91% of the excess heat. Respiratory heat loss (Eskimo $5.1\text{ Cal/m}^2/\text{hr}$; White $3.4\text{ Cal/m}^2/\text{hr}$) was constantly greater in the Eskimos because of a higher minute volume.

Kawahata et al. (1961) counted active sweat glands during maximal sweating at an ambient temperature of about 41°C in Caucasians, Negroes, and eight female and two male Eskimos of Anaktuvuk Pass, Alaska. The rank order in total number of sweat glands beginning with the lowest number was Caucasian females, Caucasian males, Eskimo females, Negro males, Eskimo males. The rank order in number of sweat glands per cm^2 of body surface area was Caucasian females, Eskimo females, Caucasian males, Eskimo males, Negro males.

Response to whole body cooling. Adams et al. (1958) exposed 6 Anaktuvuk Eskimo males, seven American Negroes and seven Caucasian soldier controls nude for 120 minutes to an air temperature of 17°C . The Eskimos had a higher metabolic rate in the control period (Eskimo 50, White 40, Negro 38 $\text{Cal/m}^2/\text{hr}$). The average rise in metabolism due to shivering was similar in the Eskimos and soldier controls (22 $\text{Cal/m}^2/\text{hr}$). The Eskimo group had higher core and shell temperatures during cooling and shivered, as did white controls, when the average skin temperature reached 29.5°C .

Tissue conductance. Covino (1960, 1961) studied thermal regulation in five Pt. Barrow Eskimos and five controls (including one American Negro) immersed in a bath calorimeter at 35°C and 33°C . The Eskimos produced more heat and lost more body heat during the immersion periods and their rectal temperatures fell to lower levels. There was no difference in digital blood flow. The greater tissue conductance was related to the significantly smaller percentage of body fat in these Eskimos.

Adipose tissue. Covino (1960, 1961) and Elsner (1960) report that the body fat content of all Eskimos is characteristically low.

Eskimo summary. Possibly owing to dietary factors (Rodahl, 1952), Eskimos have a 20% to 30% higher basal metabolism than Caucasians when S. A. (Brown et al., 1953; MacHattie et al., 1960) or lean body mass (Covino, 1960) is used as a reference standard; and this difference is maintained during shivering (Adams et al., 1958) and exercise (Rodahl et al., 1957). At high ambient temperatures or during a hard walk in the cold, sweating accounts for most of the dissipation of the excess heat (Rodahl et al., 1957). In addition, a higher minute volume results in a greater respiratory heat loss (Rodahl et al., 1957). During a whole body cold stress, the "critical temperature," which causes a rise in metabolism by shivering, is the same in Eskimos and Caucasians (Adams et al., 1958). When either legs or hands are cooled in water, blood flow is greater in the hands and forearms of Eskimos (Brown et al., 1952; Brown et al., 1953; Page et al., 1953; Meehan, 1955). The threshold for "heat" pain is the same (Meehan, 1954) but there are suggestions of a difference for "cold" pain. Tissue conductance in cold water immersions is greater because of a significantly smaller percentage of body fat and a higher heat production (Covino, 1960, 1961; Elsner, 1960). The Eskimo has a higher metabolic heat production which requires a greater potency of heat dissipation mechanisms. According to Hardy (1961) it is body temperature which is regulated by the hypothalamus, not the energy flux through the organism.

Athapascan Indians

The antiquity of the northern Athapascan tribes is presently unknown. The exigencies of a nomadic existence in a subarctic environment imposed certain arbitrary population controls; few permanent camps were established, and artifactual remains are sparse. They presently inhabit interior Alaska and Canada, where a continental type climate results in seasonal extremes in temperature. According to Sapir (1936), Newman (1954), and Kraus et al.

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(1956) language affinities between the Apaches and the Northern Athapascans indicate that the former migrated southward 400 to 600 years ago.

Response to whole body cooling. Meehan (1955) measured metabolic rates, and surface and rectal temperatures of nine male Fort Yukon natives and Caucasian controls clad in a light underwear suit and exposed for 90 minutes to an air temperature of 6°C to 7°C . Initial resting metabolic rates and respiratory quotients were close to basal values and were the same in both groups. In the cold room, the natives shivered more and had a significantly higher metabolic rate increase ($142\pm 22\%$) after 90 minutes than did the Caucasian controls ($77\pm 11\%$). The hands and feet of the natives were significantly warmer and the Caucasians incurred a greater total heat debt.

Irving et al. (1960) measured the sleeping metabolism, rectal temperatures, and skin temperatures of eleven male Old Crow Indians and seven Caucasian controls. These parameters were measured during 7 hours of warm sleep and 7 hours at 0°C with about 1 clo insulation. Initially, the Indian basal metabolism was approximately 14% higher than Benedicts' standards. By using "lean weight" as a reference, the two groups did not differ in metabolism. During the cold exposure the average elevation of metabolism in the Indian subjects was 29% and in the Caucasians 32%. During the warm nights the Indians and controls were awake 12% and 13% of the time respectively. During the cold nights the Indians were awake 49% and the Caucasians 69% of the time. During both warm and cold nights the Indians lost more heat from body storage. However, the skin temperatures of the Indians and Caucasians did not differ significantly, and no evidence was found of adaptation in metabolic rate of thermal reactions.

Elsner et al. (1960), in order to investigate seasonal differences in the Old Crow population, restudied eight male Indians in the spring. Metabolism, skin temperatures, and rectal temperatures were measured during sleep at 0°C to 3°C with 1 clo insulation. Basal oxygen consumption of four natives was approximately 10%

above DuBois standards. Metabolism increased 30% during the night; and skin and rectal temperatures declined as in the previous study. It was concluded that meager evidence for general metabolic and thermal adaptation was found by methods which revealed important differences in naked Australians and warmly dressed Lapps.

Response of extremities to cooling. Elsner et al. (1960) studied the transfer of heat via the circulation of blood to the hands of Old Crow Indian males. In the first experiment nine Indians and eight Caucasian controls immersed their right hands in 5⁰ C water for 30 minutes after a control period of 30 minutes in 30⁰ C water. These experiments were done with the subjects clothed in a warm room and unclothed in a warm room. The Indian hands transferred a significantly greater amount of heat to the water in both the warm and cold environments. In a second experiment, six Indians and five controls immersed the right hands in ice water. The Indian group had a more rapid rewarming and suffered less pain.

Meehan (1955), quoted earlier, reported warmer finger temperatures in ice water in Fort Yukon natives as compared to those of Caucasian controls.

Physical fitness. Anderson et al. (1960) investigated the physical fitness of eleven male Indians from Old Crow. Respiratory gas exchange and heart rate during steady state exercise were measured. The response of extra ventilation to a standard exercise load was also determined. The results showed that the Indians occupied an intermediate position between young sedentary Norwegians and Norwegian athletes in their fitness for work.

Athapascan Indian summary. Basal metabolic rates are the same in Athapascans as in Caucasians when compared to "lean weight" (Irving et al., 1960), but 14% higher than Benedict's standard, and 10% above DuBois standard values (Elsner et al., 1960).

Indians showed no difference in metabolic and thermal reactions when compared to Caucasian controls that were exposed to low

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temperatures during sleep in the fall (Irving et al., 1960) and the spring (Elsner et al., 1960).

Indians, even when in negative heat balance, have warmer hands in cold water than Caucasian controls (Elsner et al., 1960) and warmer fingers in ice water (Meehan, 1955).

Physically the Indians are lean (Irving et al., 1960) and occupy an intermediate position between young sedentary Norwegians and Norwegian Olympic athletes in their fitness for work (Anderson et al., 1960).

The Lapps

Lapland, which has no political existence, consists of the forested highlands of northern Sweden, tundra-covered areas of northern Finland, Norway's coastal province of Troms and Finnmark, and much of the Russian Kola Peninsula. The Lapps presently number about 35,000. They have national allegiance to the country where they are domiciled and share this country, with a larger population of Finns, Norwegians, Swedes, and Russians with whom they have been interbreeding for centuries. Historical accounts seem to indicate that the Lapps were originally hunters who in about 1500 A. D. became reindeer domesticators, having learned this art from the Samoyedie peoples to the east. According to a number of blood surveys, the Lapps have apparently reached their present genetical constitution through long isolation as a relatively small population. Norwegian Lapps have in recent centuries received a larger genetical contribution from the outside than have the Swedish Lapps.

Russian Lapland, Finnish Lapland, and the part of Swedish Lapland situated above the Arctic Circle enjoy about the same temperatures as the southern half of the Labrador peninsula because of the ameliorating effect of the warm water of the Gulf Stream upon the climate (Milan, 1960, from published sources).

The information on the physiology of the Lapps is restricted to that obtained from studies of reindeer nomads and villagers from Kautokeino in northern Norway.

Critical temperature. Scholander et al. (1957) determined the "critical temperature," i. e. the lowest temperature at which a resting metabolic rate maintained a constant body temperature, in nine male migratory Lapps from Kautokeino and three male Norwegian controls. The nude subjects bicycle on an ergometer wheel in a temperature regulated room. Rectal temperatures and oxygen consumption were monitored. The intersect of resting values of oxygen consumption and values in the cold occurred at approximately 27°C , and this was taken as the critical temperature. The subjects perceived a fall in rectal temperature as small as 0.2°C . Critical temperatures were the same in both groups.

By measuring skin temperature under the clothing of Lapps out-of-doors, it was determined that they live within a warm microclimate.

Response to whole body cooling. Lange Andersen et al. (1960) measured skin and rectal temperatures and metabolism in 14 male Lapps from Kautokeino and five male Norwegian controls during 8 hour exposure to 0°C while sleeping nude with about 1 clo insulation. The Lappish subjects consisted of five settled villagers and nine reindeer nomads. During the cold exposure, most of the reindeer nomads slept well with no obvious shivering. The controls slept poorly and suffered from surface cooling, especially in the legs and feet. The nomads and controls had similar skin temperatures, but the nomads lost more heat from the body core because of a lower metabolic heat production. The Lapp villagers were intermediate between the controls and nomads in their responses.

Response to extremity cooling. Krog et al. (1960) measured hand blood flow in a venous occlusion plethysmograph at various temperatures and hand heat loss and finger temperatures in 0°C stirred ice water. The subjects were 13 male Kautokeino Lapps, 10-12 Lofoten Island fishermen, 6-11 Gothenburg medical students, and 4 authors. Maximum hand blood flow at 40°C was similar in all subjects. Hand blood flow at 10°C and 20°C was the same in

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all subjects. The blood flow values reported in this study are considerably higher than those reported by Brown et al. (1952); these authors suggest that Brown kept his subjects cooler, and their hand flows were influenced by vasoconstrictor fiber activity. During immersion in 0° C water the temperatures of the cold habituated subjects (Lapps and fishermen) were similar to those of the controls. There was, however, an earlier onset of vasodilation in the Lapps and fishermen. Although the cold habituated subjects experienced less pain and discomfort, two Lapps and three fishermen fainted during the experiment. The results of the study did not support the hypothesis that cold habituated individuals possess a purely local vascular adaptation resulting in a greater blood flow through the hands.

Lapp summary. Kautokeino Lapps, when compared with Norwegian controls, slept well with no obvious shivering during a night exposed to an air temperature of 0° C and lost more heat from the core because of a lower metabolic heat production (Lange Andersen et al., 1960). Paradoxically, the critical temperature is the same for Lapps and Norwegian controls (Scholander et al., 1957). Hand blood flows at various temperatures and finger temperatures in 0° C water are the same for cold habituated nomadic Lapps, Lofoten Island fishermen, and controls, but the former two groups vasodilated earlier and reported less pain when vasoconstricted.

The Indians of Southern Chile

The aboriginal inhabitants of the islands in and around the Straits of Magellan in southern Chile and Argentina became famous for their cold hardiness through the writings of Charles Darwin, who visited this region in the H. M. S. Beagle. The Fuegian tribes consisted of the Chono, Haush, Ona, Vaghan, and Alacaluf. Only the physiology of the Alacalufs has been investigated.

The Alacalufs formerly inhabited the islands from the Gulf of Penas as far south as the northwest part of Isla Grande on Tierra del Fuego. This habitat is an isolated and densely vegetated region

with 120 inches of precipitation, which falls as snow in winter. It has been estimated that the Alacalufs numbered between 3500 and 4000 in 1850. Presently there are about 50 Alacalufs who are settled on Wellington Island (Bird, 1946; Cooper, 1946).

Response to whole body exposure. Hammel et al. (1960) studied nine male Alacalufs exposed for 8 hours during the night to an air temperature of 2°C to 4°C and six male Alacalufs during sleep while comfortably warm. Oxygen consumption and skin and rectal temperatures were measured. No controls were used. At the beginning of the night the metabolic rate was about 60% above the basal values for a standard white European of the same weight, height, and age. In similar circumstances a white would be no more than 20% above basal values (Hammel et al., 1959). The average metabolism during the cold nights was indistinguishable from that during the warm nights, except for occasional bursts of shivering, and metabolism gradually decreased over the 8 hour period. The Alacalufs resembled the Indians of Old Crow in their metabolic responses, which were nearly twice as great as those measured in the Australian aborigines during a similar exposure. Rectal temperatures were about the same as those measured in European controls, while skin temperatures were about 1°C lower. The feet were about 2°C to 3°C warmer. Measurements of tissue conductance in the Alacalufs showed complete vasodilation in these subjects when sleeping warm. During the cold nights, tissue conductance was halved, but it was still 30% higher than in the Australian aborigines.

Responses to extremity cooling. Elsner in Hammel et al. (1960) measured the heat output of the feet and hands of Alacaluf Indians and three white controls in cold water. The hands and feet, after an initial immersion in 30°C water, were placed in 5°C and 10°C water, respectively. The range of heat output in these subjects overlapped that of white controls. Whereas the Alacaluf men and women reported no pain, the controls experienced intense pain in the feet during the immersion.

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Alacaluf summary. The Alacalufs studied in the field have an elevated basal metabolism, and during an 8 hour moderate cold exposure their metabolism is virtually indistinguishable from that measured while warm (Hammel et al., 1960). During cooling of the feet and hands, heat loss was similar to that of white controls but pain sensation, reported as intense in the controls, was absent.

The Australian Aborigines

The land connection between Australia and the mainland of Asia was submerged during the late Pleistocene. Australia then became a refuge area for archaic forms of plants, animals, and men. It has been estimated that the continent has been inhabited for about 15,000 to 20,000 years, and its human population has been described as tri-hybrid in origin, representing an amalgamation of archaic Caucaoids, Veddooids, and Australoids (Birdsell, 1950). This human population lived in virtual isolation until the first European settlement was established in Botany Bay in 1787. At the time of first European contact, the aborigines numbered about 250,000 in some 500 tribes, and they were naked (Elkin, 1954). In 1956 there were an estimated 60,000 aborigines in the population at large (Smythe et al., 1956).

Winter night temperatures in Central Australia fall to freezing or below, and the night sky radiation temperature is about 20°C lower. The aborigines who formerly slept naked on the ground between small fires were chronically exposed to cold.

Sir Stanton Hicks et al., (1931, 1933, 1934, 1938a, 1938b) and Goldby et al. (1938) initiated the pioneer studies of temperature regulation in the aborigines. Morrison (1957), while studying marsupials in Central Australia, measured aboriginal body temperatures. Scholander et al. (1958) and Hammel et al. (1959) have used more precise methods in extending and confirming the early data.

Observations during sleep in the natural state. Hicks et al. (1934) measured oxygen consumption and skin temperatures in sleeping male natives in Central Australia. They found that the metabolism of the natives was not elevated by the cold of early morning

and that skin temperatures were low. They postulated a more effective vasomotor control than that of civilized individuals. After the ingestion of raw meat, the SDA of protein resulted in an 80% rise in metabolism after 5 hours. The RQ was measured as 0.7 in fasting subjects and moved toward unity after a meal.

Morrison (1957) used a Stoll-Hardy radiometer to measure skin temperatures in sleeping aborigines at Haast's Bluff in Central Australia. He concluded that the aborigines had a lower sensitivity to cold, which allowed them to sleep despite low body temperatures.

Scholander et al. (1958) studied the Pitjandjara tribe which inhabits the deserts of Central Australia. Two natives and two European controls slept naked "proper bush style," lying on the ground between two fires in winter. Neither Australians nor Europeans elevated their oxygen consumption, although the Europeans were uncomfortable and did not sleep well. The natives stoked their fires three to ten times while the Europeans stoked eleven to fourteen times. The natives tolerated a lower average skin temperature.

In a second experiment four Europeans and six natives slept naked in a bag of 1.9 clo insulation on a canvas cot under a thin radiation shield. Night temperatures were between 5° C and 0° C. The metabolism of the natives fell below basal values during the night, whereas the Europeans elevated their metabolism by bursts of shivering. The natives slept, while the European controls were kept awake by cold feet, although the natives had lower skin temperatures. It was concluded that the natives had adapted both their technology and physiology to withstand chronic cold exposure.

Hammel et al. (1959) returned to study the Central Australian natives in summer to see if the differences reported by Scholander et al. (1958) were seasonal. In addition, natives from the tropical north coast with a history of little cold exposure were studied. Eight male Pitjandjara, nine male tropical natives, and seven male European controls were exposed during sleep in a 1.7 clo bag in a refrigerated meat van for 8 hours at 5° C. The metabolism of the Pitjandjaras was lower than that of the European controls. The tropical natives were intermediate in metabolic response. The Pitjandjaras

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allowed greater cooling of the core and shell, their thermal conductance was significantly less, and their average skin temperatures were considerably lower. The low tissue conductance in the tropical natives resulted in skin temperatures which were intermediate between those of the Europeans and Pitjandjaras. The rectal temperatures were the same in the tropical natives and European controls. It was concluded that the Australian aboriginals had an inborn ability to tolerate greater body cooling without recourse to metabolic compensation and that this tolerance could be increased by prolonged exposure to cold.

Australian summary. Australian aborigines lying naked on the ground find low skin and rectal temperatures compatible with sleep (Hicks et al., 1934 and Morrison, 1957). Central Australian aborigines, when contrasted with European controls in a moderately cold sleeping environment, do not elevate their heat production despite low skin and rectal temperatures either in winter (Scholander et al., 1958) or summer (Hammel et al., 1959).

The American Negroes

American Negroes were transported as slaves from the old empires of Ghana, Melle, and Songhay in West Africa. The Negro-American population is by no means pure, and it is considered a race in the process of formation by several recent authors (Coon et al., 1950).

Responses to whole body cooling. Rennie et al. (1957) exposed eight male Caucasian soldiers and eight male American Negro soldiers for 90 minutes to -12°C in summer and winter. Subjects were clothed except for hands and fingers. The Caucasians had a higher heat production, and the increase in metabolism was delayed in the Negroes. After 70 minutes the Negro rectal temperature was significantly lower. Although the average skin temperature was the same, the Negro hands and feet were colder.

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Adams et al. (1958) contrasted the metabolic and thermal responses of six male Eskimos, seven male Negro soldiers, and seven male Caucasian soldier controls exposed nude for 120 minutes to 17°C . While the Eskimos and Caucasians shivered at a mean skin temperature of 29.5°C , the Negroes did not shiver until their skin temperatures reached 28°C . Skin temperatures were the same in the Negro and control groups, but the metabolic response was greater in the latter.

Iampietro et al. (1959) matched 16 male American Negro soldiers with 17 male Caucasian soldiers for percentage fat, height, weight, etc. and exposed them nude for 2 hours to 10°C . Metabolic responses were the same. Although the difference between groups in average skin temperatures approached significance after 100 minutes (Negroes were 0.8°C lower), other temperatures were the same.

Response to extremity cooling. Meehan (1955) measured temperatures of index fingers immersed for 30 minutes in stirred ice water in 52 Alaska natives, 38 American Negroes, and 168 Caucasians and reported that Negroes maintained the lowest temperatures. Iampietro et al. (1959) measured temperatures of fingers in ice water in 16 male Negro soldiers and 17 male Caucasian soldiers. The white subjects had higher finger temperatures, and the "hurting" reaction was more pronounced.

Negro summary. The metabolic and thermal responses of American Negroes were reported to be different from those of white controls during a standardized cold stress of -12°C while clothed (Rennie et al., 1957) and 17°C while nude (Adams et al., 1958) but the same when nude at 10°C (Iampietro et al., 1959). The fingers of Negroes immersed in ice water are cooler than those of white controls (Meehan, 1955; Iampietro et al., 1959).

The Bushmen

Presently the Bushmen number approximately 55,000. They

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occupy a small fraction of their former territory and are found in South West Africa, Bechuanaland Protectorate, Angola, Rhodesia, and the Republic of South Africa. They are hunters and gatherers, lighter in color than their Bantu neighbors, and speak a Click language. In physical appearance they are short of stature (4 feet 9 inches to 5 feet 4 inches) and have a number of anatomical infantile features (Tobias, 1961).

The Bushmen were formerly distributed over much of southwest Africa but are presently confined to the high plateau of the Kalahari Desert at altitudes between 3000 and 5000 feet. Here the winter night climate is sufficiently cold to be stressful for a habitually naked people.

Response to whole body cooling. Wyndham et al. (1958) measured the skin and oral temperatures of two male Bushmen and two white South Africans sitting nude for two and one half hours. Ambient temperatures ranged between 10°C and 15°C . The oral temperatures of the Bushmen were lower. The skin temperature of one bushmen sleeping naked under his cloak next to a fire was measured for 8 hours. Ambient temperatures ranged between 12°C and 13°C . Air temperatures under the cloak were about 26°C , and temperatures on the trunk were about 35°C . It was concluded that the Bushmen have made an intellectual rather than a physiological adaptation to diurnal temperature changes.

Ward et al. (1960) measured the metabolism and skin and rectal temperatures in eight male Bushmen and five male European controls exposed naked to the Kalahari Desert night environment. Night temperatures ranged between 22°C and 2.7°C . A radiation shield was interposed between the subjects and the night sky. A thermocouple on a plastic holder manipulated by an observer was utilized to obtain skin temperatures. Face masks and a Douglas Bag were used to sample metabolism intermittently. The metabolic response in the Bushmen was higher than in the controls, but the percentage increase related to skin temperature was the same for the controls, Bushmen, and Norwegians (Ward et al., 1960). Rectal temperatures were similar. The Bushmen's skin temperatures were lower because

of less body fat. It was concluded that the Bushmen had not adjusted physiologically to the climate, but that they created a local climate around them, using the meager available materials.

Bushmen summary. While sleeping on the desert in his native environment, the Bushman utilizes an artificial microclimate to avoid cold exposure. Limited tests of skin and oral temperature decline in response to cold stress revealed no difference between Bushmen and controls (Wyndham et al., 1960). Bushmen subjected to moderate cold stress while sleeping nude for short periods have similar metabolic and thermal responses to those of controls (Ward et al., 1960).

ARTIFICIAL ACCLIMATIZATION OF MAN TO COLD

The results of experiments undertaken to artificially acclimatize man to cold or to study the effects of chronic cold exposure upon soldiers or arctic and antarctic sojourners, which complement the findings of cold adaptation in chronically cold exposed natives, will be briefly reviewed. Extensive and recent reviews of the literature on the effects of cold on man are those of Burton et al. (1955), Carlson (1954), Carlson et al. (1959) and Hardy (1960).

Scholander et al. (1958) exposed eight inadequately clad male Norwegian students to low ambient temperatures in the mountains of Norway for six weeks in September and October. Metabolism and skin and rectal temperatures were measured at night while the subjects slept with 2 clo of insulation at an air temperature of 3° C. Their responses to the cold stress while sleeping were contrasted with those of 12 male controls. The acclimatized men had higher skin temperatures, especially in the feet, and they were able to sleep. They shivered in their sleep, whereas the controls did not sleep at all. A slight but transient elevation of basal metabolic rates and a

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2°C to 3°C lowering of the critical temperature occurred in the acclimatized.

Le Blanc (1956) found a significantly decreased oxygen consumption in cold acclimatized soldiers as compared with that of nonacclimatized controls when both were exposed to a series of standard acute cold stresses. He suggested that acclimatization is associated with a lowering of the body thermostat to more economical levels.

Milan et al. (1961) studied antarctic sojourners who spent a year at Little America V. The metabolic rates and the thermal responses of eight subjects (who served as their own controls), exposed nude to 17°C air temperature were measured over the year. Mean body and average skin and foot temperatures increased significantly over the year, while there was a decrease in heat production to meet the same thermal demands since shivering diminished.

Davis et al. (1961) exposed six male white subjects nude to 13.5°C air temperature in a cold room 8 hours each day for 31 days (except Sunday) in September and October. At the end of this period, metabolism remained between 35% and 75% above basal values, but shivering decreased. Skin temperatures were unchanged.

In a similar experiment, Davis et al. (1961) exposed ten male white subjects to 11.8°C for 31 days in March. At the end of this period, rectal temperatures had decreased (37.2°C to 36.7°C), skin temperatures were unchanged, and although metabolism was unchanged, shivering decreased. These authors suggest that these are indications of non-shivering thermogenesis.

Adams et al. (1958) and Heberling et al. (1961) have demonstrated that elevated skin temperature during cold stress may be a result of an increase in physical fitness.

Trends

Although it is difficult at first glance to generalize about these experiments investigating acclimatization and adaptation, there are certain trends which are apparent:

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(1) An increased ability to draw upon body heat stores.

(2) Vascular changes in the hands and feet in order to maintain warmer extremities.

(3) A diminution of shivering, a moderate cold stress possibly related to what Elsner (1960) has termed "habituation."

(4) A transient elevation of the BMR, resulting from an ability to shiver while sleeping.

Native peoples investigated are either naked or thinly clad exposed to moderate cold--the Australians, Bushmen, and Alacalufs, or heavily clothed exposed to extreme cold--Lapps, Eskimos, and Arctic Athapascans.

These cold adapted peoples show:

(1) A form of insulative cooling with a decreased tissue conductance.

(2) A metabolic sparing with the ability to draw upon body heat stores.

(3) An elevated basal metabolic rate.

(4) A decreased perception of cold sensation.

(5) An increased peripheral blood flow.

This then brings us to a recent study done in collaboration with Drs. Hannon and Evonuk.

HUMAN RACIAL RESPONSES

A COMPARATIVE STUDY OF THERMOREGULATION IN ESKIMOS, INDIANS, AND U. S. SOLDIERS

Subjects

The subjects for these experiments were six American white soldiers, six Alaskan Eskimos, and six Athapascan Indians. Their physical characteristics are presented in Table I.

Cold Exposure

The soldiers had been in Alaska less than ten days, had arrived from training camps in the southern states and, except subject 1, were all born in the Southern U. S. Their previous cold exposure was very negligible.

The Eskimos came from the isolated village of Anaktuvuk Pass in the Brooks Range and earned their livelihood by hunting and trapping land animals. They pursue a relatively vigorous existence in a cold climate.

The Indians came from the village of Tetlin, Alaska, on the Upper Tanana River. This is a region of climatic extremes and the lowest winter temperature in North America has been reported from this general area. Aboriginally these people were nomadic hunters; presently they are engaged in trapping and wood cutting, receive governmental subsidies, and are not as active in the cold as formerly.

Methods

These experiments were conducted in November, December, and January. Four and five days after they had arrived at the laboratory and had been subsisting on a hospital cafeteria diet, duplicate measurements of basal metabolic rates were made on the Eskimos and

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Subj	Age	Wt. kg	Ht. cm	S.A. m	Total Skinfold mm	% Adiposity	% Fat	Lean Body Wt. kg
<u>Soldiers</u>								
G.	24	65.8	177.8	1.82	58	23	14	50.7
K.	24	75.4	179.0	1.93	51	22	14	58.9
F.	21	77.3	183.0	2.00	49	22	14	60.3
R.	24	64.3	176.0	1.79	43	21	13	50.8
L.	24	78.4	178.8	1.96	50	22	14	61.2
B.	26	93.2	180.4	2.15	172	41	25	55.0
<u>Indians</u>								
A.	18	52.7	169.4	1.59	17	13	8	45.9
M.	19	55.1	168.3	1.62	37	19	12	44.7
J.	19	65.0	174.0	1.79	24	15	9	55.3
T.	19	70.0	171.4	1.82	35	19	12	56.8
D.	36	70.9	175.2	1.86	53	23	14	54.6
J.	28	79.3	171.5	1.92	90	30	19	55.5
<u>Eskimos</u>								
R.	25	55.9	159.0	1.56	19	13	7.5	48.7
A.	29	62.1	166.5	1.68	27	16	9.9	52.2
P.	23	61.9	161.0	1.65	13	11	6.8	53.9
M.	19	64.1	164.9	1.70	6	5	3.1	60.9
K.	29	68.7	172.6	1.82	9	9	5.5	62.5
A.	23	64.3	175.2	1.78	12	11	6.8	57.2

Table I. Physical Characteristics of Subjects.

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Indians. The subjects were in a basal state, and the measurements were made on the subjects in their own beds immediately after they had been awakened.

The subjects exhaled through a rubber mouth piece, a one way plastic valve, and a short length of rubber hose into the portable Muller-Franz respirometer described by Lehman (1953), and Montoge et al. (1958). Aliquot samples of expired air, which were about 0.3% of the total volume, were passed through Alcoa Alumina desiccant in a 50 cc glass syringe into a Model C Beckman Oxygen Analyzer. Expired air volumes at BTPS were reduced to STPD. Heat production was calculated from the following expression by the method proposed by Weir (1949):

$$\text{kcal/hr/m}^2 = \frac{V_E \times (1.046 - 0.05\% \text{O}_2\text{E}) \times 60}{\text{S. A.}}$$

where:

V_E = minute volume of expired air

$\% \text{O}_2\text{E}$ = % oxygen in expired air

S. A. = surface area in m^2

Bath calorimeter. The thermoregulated recirculating water bath calorimeter constructed and previously described by Carlson (1961) was utilized. It was similar to that used by Burton (1936). The bath contained 396 liters of water, and its temperature could be regulated within $\pm 0.1^\circ \text{C}$. The bath was installed in a room where the room air temperature could be controlled within $\pm 1.0^\circ \text{C}$. Water temperatures selected were 35°C , 33°C and 30.5°C , and room temperatures were maintained about 14°C lower to insure a constant rate of heat loss. Water and room temperatures were allowed to stabilize for 12 hours. The average amount of electrical energy required to maintain the water temperature in the calorimeter was measured at 6

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minute intervals. The factor 0.86 was used to convert watts to kcal/hr (Handbook of Chemistry and Physics).

The subject reclined in the bath with all except his face immersed in water. The subject's total heat loss was determined with a correction applied equal to the caloric equivalent of the water displaced by the subject. Total immersion time was one hour. Although heat production did not equal heat loss during this hour and true steady state conditions were not achieved, rates of change were constant during the last 30 minutes, and these data were used. This period is what Burton (1939) has termed a "dynamic steady state."

Heat production. Heat production was continuously monitored by the respirometer-oxygen analyzer combination utilized to measure basal metabolic rates.

Rectal temperature. An indwelling catheter type thermistor was inserted 10 cm into the rectum and secured to the buttock by waterproof tape. Temperatures were measured on a Yellow Springs Instrument Co. Telethermometer and recorded on the strip chart of an Esterline Angus Recorder.

Calculation. The Laws of Heat Transfer by Thermal Conduction have been summarized by Hardy (1949) and are analogous to Ohm's Law for electrical circuits. The fundamental equation for heat conduction in the steady state is:

$$H_D = \frac{KA(T_2 - T_1)}{d} \times t, \text{ gm cal}$$

where:

H_D = quantity of heat conducted

K = thermal conductivity, a constant

A = area of conducting surfaces

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T_2 and T_1 = temperatures of the warm and cool surfaces

t = time

d = thickness of the conductor

It follows that tissue insulation may be determined from the equation:

$$K_i = \frac{(T_r - T_w)}{H}$$

where:

K_i = tissue insulation $^{\circ}\text{C}/\text{kcal}/\text{m}^2/\text{hr}$

T_r = average rectal temperature

T_w = water temperature

H = heat loss ($\text{kcal}/\text{m}^2/\text{hr}$) measured over 30 minutes

For these calculations it is assumed that skin temperature is equal to water temperature and that regional gradients over the body have been obliterated. Although this assumption disregards the temperature of the boundary layer between the skin-water interface, the assumption has precedents (Carlson et al., 1958; Covino, 1960).

Determination of Body Fat

The skin fold calipers described by Best (1953) were used to measure the thickness of ten double folds of skin and subcutaneous fat at the sites recommended by Allen et al. (1956). Percentage of adiposity was determined from the total skinfold thickness minus 40 mm (the thickness of ten double folds of skin) according to Allen's formula. Percentage of adiposity was multiplied by 0.62 which corrected for water in adipose tissue (Brozek et al., 1954).

Statistical Treatment

These data were analyzed in a single classification analysis of variance.

RESULTS

Basal metabolic rates. Average basal metabolic rates and standard deviations were 47.6 ± 4.41 and 45.4 ± 4.91 kcal/m²/hr for the Eskimos and 42.7 ± 1.70 and 42.2 ± 3.92 kcal/m²/hr for the Indians. The basal metabolic rates of the soldiers were not measured. Lewis et al. (1961) have reported a mean value of 37.4 ± 3.66 kcal/m²/hr for 349 measurements on 29 British men with an average age of 29 years. This figure is close to the average metabolism of the soldiers in the 35° C bath. Each hour the Eskimos produced about 8 to 10 kcal and the Indians about 5 kcal more than the soldiers when surface area was used as the metabolic reference standard.

Calorimetric studies. A summary of the data showing the manner in which the three groups are similar or differ, and the level of significance attached to these differences is shown in Table 2. It is of more than passing interest that although there were no differences in the fall of rectal temperatures, the Eskimo group, in general, produced and lost the greatest amount of heat in the water baths at all temperatures.

The relation between an index of "effective thermal conductivity" and the physiological temperature gradient across which the energy is transferred is shown graphically for all subjects in Figure 1. The relation between tissue insulation, actually the reciprocal of conductivity, and the temperature gradient is shown in Figure 2.

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35° C BATH						
	SOLDIERS	INDIANS	ESKIMOS	E vs I	I vs S	E vs S
M	36.9	42.8	50.3	<.02	<.05	<.001
L	51	47	73	<.001	>.10	<.001
ΔT_R	-0.21	-0.38	-0.32	>.05	>.05	>.05
K_i	.029	.032	.021	<.001	<.05	<.001
33° C BATH						
M	39.4	50.9	54.7	>.10	<.01	<.01
L	66	62	86	<.001	>.50	<.01
ΔT_R	-0.46	-0.67	-0.56	>.05	>.05	>.05
K_i	.052	.053	.038	<.001	>.50	<.001
30.5° C BATH						
M	48.1	52.8	62.8	>.10	>.50	<.05
L	86	75	94	<.001	<.05	>.05
ΔT_R	-0.7	-0.9	-1.1	>.05	>.05	>.05
K_i	.071	.068	.057	<.001	>.05	<.001

Table II. Average values of metabolism (M) and heat loss (L) in kcal/m²/hr, fall in rectal temperature (ΔT_R) in °C and tissue insulation (K_i) in °C/kcal/m²/hr for the three groups at the three bath temperatures. P values show the levels of significance which can be attached to the between group differences.

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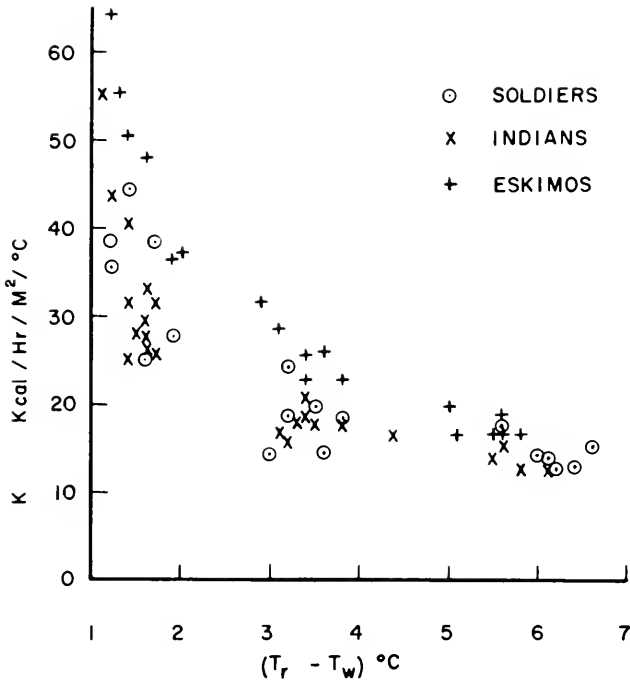


Figure 1. A graphical illustration of the relation between an index of thermal conductivity and the physiological temperature gradient.

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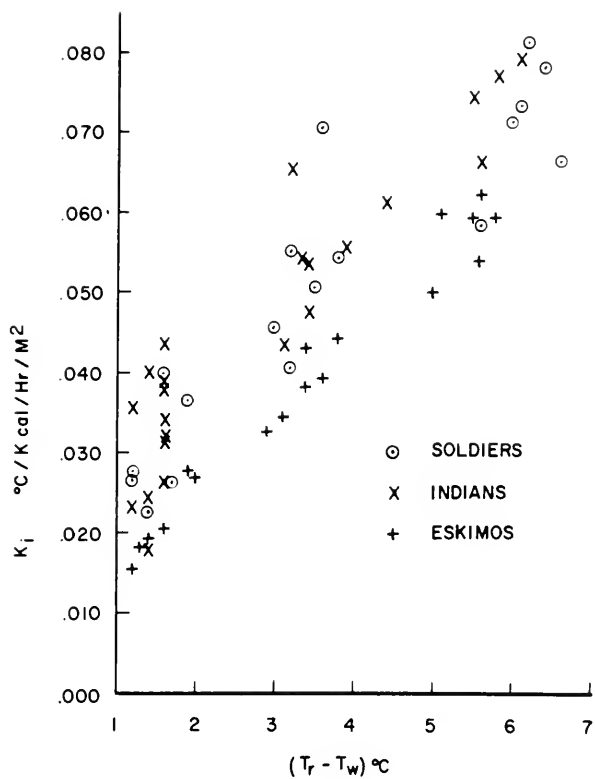


Figure 2. The relation between tissue insulation and the physiological temperature gradient.

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In Figure 3 is shown the relation between tissue insulation and the three bath temperatures. At all temperatures the Eskimos have significantly lower tissue insulations than the other groups. The Indians and soldiers are similar to each other and indistinguishable at 33°C . The three extrapolated curves intercept at about 36.5°C and at this bath temperature, under the conditions of this study, tissue insulation would presumably equal zero.

Percent body fat. The mean values for percent fat in the Eskimos, soldiers, and Indians were 6.6, 15.6 and 12.3. Although the Indians and soldiers were not significantly different from each other, the Eskimos were considerably leaner in body build. Coefficients of the regression line of tissue insulation versus percent body fat were 0.847, 0.309 and 0.657 at 35°C , 33°C and 30.5°C respectively. An analysis of covariance was then undertaken in which tissue insulations were adjusted for their regressions on percent body fat. At 35°C there were no differences between groups. At 33°C the differences were significant at the .05 level. At 30.5°C the differences were significant at the .01 level.

DISCUSSION

These experiments show that there are differences in total body heat loss and heat production between a sample of Eskimos, Indians, and soldiers immersed in temperature regulated baths. Although rates of heat loss and production were unchanging during the 30 minute period of measurement, the most serious criticism of the results of this experiment concerns non-steady state conditions, for rectal temperatures were falling.

It should be noted that there were no inter-group differences in the fall of rectal temperatures despite considerable differences in heat loss and production. In the 33°C bath the differences in

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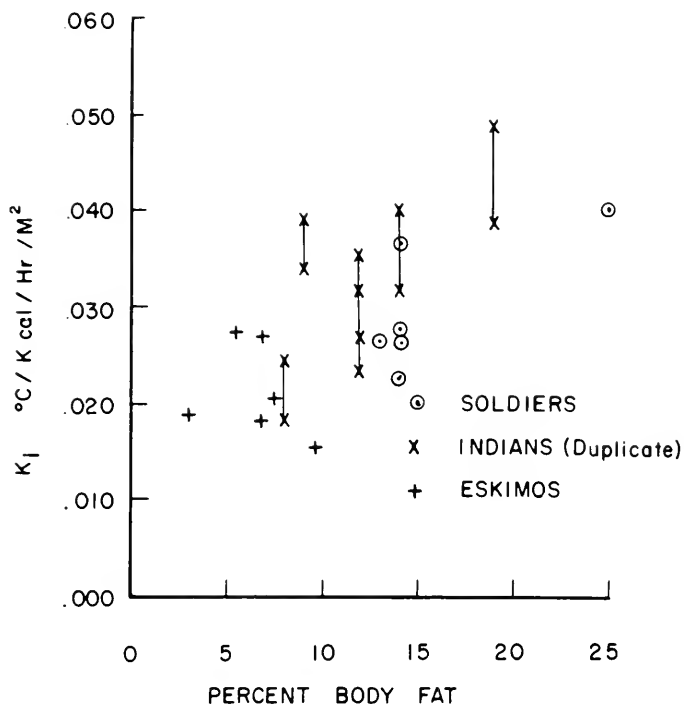


Figure 3. The relation between tissue insulation and bath temperatures.

total heat loss and production between the soldiers and the Eskimos were highly significant. The first law of thermodynamics allows us to say that $M \pm D = H$ where M = metabolism, D = heat debt, and H = the combined losses of heat through conduction, convection, radiation, and evaporation (Carlson, 1954). We can assume that about 8% of M is evaporative heat loss. In the 33° C bath, then, Eskimo and soldier average metabolisms are 54.7 and 39.4 kcal/m²/hr. By subtracting 8% of these values we see that the Eskimos have 50 kcal/m²/hr and the soldiers 36 kcal/m²/hr available to lose to the colder bath water without incurring a heat debt. They lost 86 and 66 kcal/m²/hr, a difference of 20 kcal, and incurred body heat debts at the same rates. The differences between heat produced and total heat loss is then 36 kcal for the Eskimos and 30 kcal for the soldiers. The Eskimos are characterized by a greater energy flux through the system (a system which can be described as an isothermal energy converter). In addition a greater mass of the Eskimo peripheral tissue participates in this cooling. It is tempting to conclude that the Eskimos have smaller "cores" and larger "shells."

Others (Carlson et al., 1958; Pugh et al., 1960; Cannon et al., 1960) have shown that subcutaneous fat is of considerable importance in reducing heat loss in cold water. Hatfield et al. (1951) have reported that the thermal insulation of 1 cm of fat is $\frac{1}{0.0005}$ kcal/cm²/sec. The experiments of Cannon et al. (1960) showed that fat men achieved a higher maximum tissue insulation in cold water than thin men. Carlson et al. (1958) have reported tissue insulations that range between 0.10° C/kcal/m²/hr and 0.40° C/kcal/m²/hr. Carlson's values are considerably higher than the tissue insulations reported here and are probably more nearly correct for steady state conditions above the critical temperature.

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DISCUSSION

ADAMS: Would your metabolic rates measured in the bath calorimeter compare with those measured under basal conditions?

MILAN: I would say they would be about the same.

HANNON: Were your basal metabolic rates measured under bed rest conditions?

MILAN: Yes, and I think, as pointed out by Henderson in 1926, that there is a relationship between basal metabolic activity and the circulation. Thus, if you have a slightly higher basal metabolism, the energy flux is somewhat different, since if you subscribe to the view of Hardy (1961) the hypothalamus regulates for temperature, not energy flux.

KLEIBER: I notice that there is a discrepancy from data published by Swift,* who reported that his college students began shivering when their skin temperatures went down to 90° F. But now the newer data seem to indicate that practically all human beings have much higher skin temperatures at a critical level than the level at which the metabolic temperature regulation starts. Is there an answer to this discrepancy?

MILAN: I do not know.

ADAMS: I might offer one suggestion: the method of taking the average skin temperature makes quite a difference, if this measurement was calculated in such a way as to give proportionalities to each site different from conventional standards.

*Swift, R. W. 1932. The effect of low environmental temperature upon metabolism. II. The influence of shivering, subcutaneous fat, and skin temperature on heat production. *J. Nutr.* 5:227-229.

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KLEIBER: I was tempted to conclude that these college students had a non-shivering metabolic increase, but this is a dangerous conclusion.

JOHANSEN: I was thinking of the rather profound seasonal changes in BMR that Yoshimura has reported for his Japanese subjects. Is this not out of proportion with what has been found in other populations?

MILAN: Yes. Professor Yoshimura said, when he was here, that he tried to do his studies under strict basal conditions, and I think the Japanese spend more time and efforts on their measurements of basal metabolism than we do.

PROSSER: Would you conclude that these higher BMRs in the Eskimos are not related to specific dynamic action?

MILAN: I should hesitate to conclude anything. I know only that the experiments of Rodahl (1952) indicated that the high Eskimo BMR was related to the high protein diet and possibly the specific dynamic action of this diet. However, the recent experiments of MacHattie et al. (1960) which investigated the 24 hour metabolism of the Anaktuvuk Eskimos seem to indicate otherwise. Heat production and the energy fraction contributed by catabolism of carbohydrate, fat and protein were determined by indirect calorimetry and measurements of urinary nitrogen. They reported no correlation between the rate of night metabolism and the amount of protein or fat fuel energy fraction and suggested that other factors than specific dynamic action were involved as the cause of the elevated resting metabolism of these people.

HANNON: In your particular experiments the BMRs are measured after 5 days on a hospital diet. Therefore if the elevated metabolic rate is due to a specific dynamic action it would seem to have lasted over a period of 5 days.

HART: I wanted to ask about this, too, because we had some occasion from our Eskimo studies at Pangnirtung to see long lasting effects even on some people who are living on a white man's diet

MILAN

for 4 or 5 days. They still had a 25% elevation in heat production. Is there any explanation for this? I do not understand how dynamic action can last so long.

EAGAN: Yoshimura, Iida and Koishi (1952)* have shown that when the protein fraction in the diet is increased there is an increase in BMR which persists for several days after the protein intake is reduced to normal. This result was obtained by merely doubling the protein intake from a normal 75 grams to 150 grams per day.

MORRISON: What is the implication of this? Are the amino acids stored away and then used gradually? Would the high protein diet encourage their storage?

HANNON: There is a very confusing picture with respect to the mechanism of specific dynamic action. We attempted to get at this one time by infusing an animal intravenously with amino acids to see how they affected his metabolism. Nothing happened, so we discontinued the experiments.

MORRISON: Nothing happened? Are there not reports in literature showing that infused amino acids give a normal specific dynamic action?

HANNON: This was intravenous infusion where two different amino acids--glycine and glutamate--were tested. Neither caused any increase in the metabolic rate. It is interesting that you do get the specific dynamic action when the animal eats protein. This might suggest that the mechanism of SDA may have something to do with gut absorption; I do not really know.

ADAMS: This picture on the SDA effect of glycine is really confused. Dr. Carlson tried feeding glycine and noted a subsequent

*Yoshimura, H., T. Iida and H. Koishi. 1952. Studies on the reactivity of skin vessels to extreme cold. Part III. Effects of diets on the reactivity of skin vessels to cold. Jap. J. Physiol. 2:310-315.

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increase in metabolic rate, if I remember correctly. In similar experiments we did not see anything in Caucasian soldiers. In a racial study of Eskimos from Anaktuvuk Pass a few years ago we observed a maintenance of the raised metabolic rate even after living for 2 weeks on Ladd Air Force Base and eating in the hospital. The problem of course is they were on an ad libitum diet and we had no idea of the proportions of the various foods that they selected for their meals or the supplemental foods they may have eaten in town. However there was no apparent change in metabolic rate from when they first brought them down to when they left.

HANNON: It has been my observation, from watching them in the hospital cafeteria line, that they avoid salads and green vegetables. They like potatoes and meat, so they may not be changing the nature of their diet as much as you might anticipate.

HART: Dr. J. A. Hildes (University of Manitoba) and I measured the metabolic rate of coppermine Eskimos who had been hospitalized at Edmonton, Alta., for several months. We measured the metabolic rate of coppermine Eskimos who had been hospitalized at Edmonton, Alta., for several months. We measured metabolism all night in the sleeping situation and found that it was identical to that specified by the DuBois standards corresponding to the weight and height of these men. There did not seem to be any long term elevation of BMR after they had been living under white man's conditions.

HANNON: Are these ambulatory patients or bed patients?

HART: They were hospitalized, but there were no active tuberculosis among the test subjects. They had been suffering various ailments, but nothing of a severe metabolic nature.

ADAMS: How long had they been down?

HART: This varied a great deal.

IRVING: Some of them were chronic, almost permanent?

HART: Yes. Others were there for several months.

MILAN

ADAMS: It might be important to notice the proportional adjustment of their diet.

HART: These men were eating a normal white man's diet.

HANNON: Your controls were in the same place?

HART: There were no controls in this case. It was just the Eskimo compared to DuBois standards.

ADAMS: I do not feel, as Dr. Rodahl pointed out in the recent reviews, that anxiety plays too much of a role in these basal metabolic rates. In repeated examinations you would expect the effects of anxiety to be reflected by a successive reduction in the metabolic rate. Thus it may have an effect in one or two measurements, but not after a series.

HART: That is my impression.

MILAN: Dr. Hannon, there has been considerable interest in the vascular responses of people who have been acclimatized or habituated to a cold bath, and Dr. Eagan has some information that was obtained on the subjects we had here last winter. I wonder, since we have some time left, if he might present some of the data he obtained.

HANNON: All right.

HUMAN RACIAL RESPONSES
LOCAL COLD ADAPTATION AND HABITUATION

C. J. Eagan

When experiments are done on any animal that is conscious of its environment, the role of the higher nervous centers in modifying physiological responses cannot be ignored. Bernard (1865)* in "An introduction to the study of experimental medicine" (1927) has stated:

no animal is ever absolutely comparable with another--
neither is the same animal comparable with himself at
different times when we examine him, whether because
he is in different conditions, or because his organism
has grown less sensitive, by getting used to the substance
given him or to the operation to which he is subjected.

Davis (1934)** described modifications in the galvanic reflex as a result of daily repetition of a stimulus. Other examples could be cited. A progressive reduction in response to a repeated stimulus has been termed "habituation" by Glaser and Whittow (1953)***. "Habituation" is defined as "the process of forming into a habit or accustoming" and it is implied that "it depends on the mind, that it is reversible, and that it may involve the diminution of normal responses or sensations" (Glaser, Hall, and Whittow, 1959****).

This is a type of adaptation. Where the habituation is characterized by a reduction in response to a cold stimulus, then it is a "cold adaptation." In man it may be the most common type of cold adaptation which occurs.

I propose that there are two types of habituation, specific and general. "Specific habituation" is specific to the repeated stimulus

*Bernard, C. 1865. An introduction to the study of experimental medicine. Henry Schuman, Inc. 1927. 226 pp.

**Davis, R. C. 1934. Modifications of the galvanic reflex by daily repetition of a stimulus. J. Exp. Psychol. 17:504-535.

***Glaser, E. M. and G. C. Whittow. 1953. Evidence for a non-specific mechanism of habituation. J. Physiol. 122:43P.

****Glaser, E. M., M. S. Hall, and G. C. Whittow. 1959. Habituation to heating and cooling of the same hand. J. Physiol. 146:152-164.

and specific to the part of the body which is repeatedly stimulated. "General habituation" might be explained as a change in the psychological "set" of the subject relevant to the conditions of experimentation so that he is no longer apprehensive, either consciously or unconsciously, at the time of the test.

These two types of habituation can develop simultaneously. Both depend upon a change in the manner in which the central nervous system interprets its afferent impulses. Both involve a progressive diminution in response to a repeated stimulus. Where the stimulus is the application of severe cold, specific and general habituation are manifested by reduced pain sensation and by reduced vasoconstrictor activity, respectively.

Both types of habituation as well as a local vascular adaptation were demonstrated in experiments done at the Arctic Aero-medical Laboratory (Eagan, 1960a*, 1960b**, 1961***). In all experiments, regimens of unilateral cold exposure ("test" side only) followed by simultaneous bilateral comparison ("test" vs. "control") were used in investigations of local tissue cold adaptation in the fingers of man. A summary of these experiments follows.

Chronic hand cooling of moderate intensity (12 hours per day with finger temperature between 10°C and 15°C for ten

*Eagan, C. J. 1960a. Topical adaptations to cold in the extremities. Proc. XI Alaskan Sci. Conf. pp. 184-185.

**Eagan, C. J. 1960b. Unilateral cold adaptation to recurrent ice water immersion. *Physiologist*, 3(3):51.

***Eagan, C. J. 1961. Habituation to recurrent ice water immersion of the finger. *Physiologist*, 4(3):31.

HUMAN RACIAL RESPONSES

days) resulted in a less intense initial vasoconstriction, less variability in digital blood flow and a 17% greater average heat loss, during a 30-minute period of ice-water immersion. Fingers of the test hand cooled more slowly than the control fingers during exposure to cold air. Pain sensation tended to be less for the test hand, especially for the fingers; this type of cold adaptation was termed "specific habituation"--specific to the cold stimulus and to the part of the body stimulated.

Recurrent finger cooling of severe intensity (six 5-minute ice-water immersions per day for 17 days) caused a marked, specific habituation to cold pain. There was no essential difference between the vascular reactions of test and control fingers when they were tested in ice water. Prolonged recurrent finger cooling (six 10-minute ice-water immersions per day for 125 days) confirmed the finding that specific habituation to pain could develop in the absence of local vascular cold adaptation. However, the subjects did show higher finger temperatures (test and control fingers alike) in ice water, compared with other subjects being tested for the first time. This was concluded to be a "general habituation" to the conditions of the experiment which resulted in less vasoconstrictor outflow to fingers in ice water.

It is considered that the results on general habituation are highly relevant to what has been discussed above by Milan. Many racial differences in the responses of the extremities to cooling have been attributed either explicitly or implicitly to localized vascular adaptations. These differences may on the contrary be related to the degree of habituation to cold exposure and the experimental conditions. Further, the energy state of the subject at the time of the test is not always taken into account.

A comparison of the responses to finger cooling in four groups of subjects is demonstrated in Table III and Figure 4.

The habituated group consisted of the six USAF airmen who had each immersed one middle finger in ice water 750 times over the

AVERAGED RESPONSES FOR 4 GROUPS (6 subjects in each) DURING
STANDARD IMMERSION OF FINGERS IN 0.0°C WATER

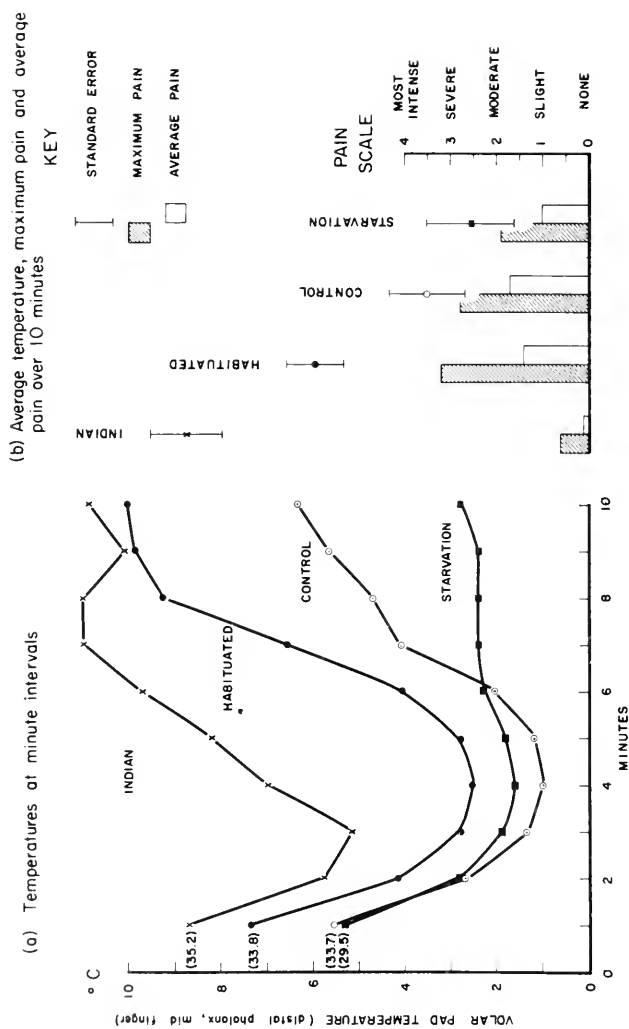


Figure 4. Comparisons of temperature and pain responses on four groups of subjects. The average responses of the control fingers of the habituated group on days are compared with the responses of the right middle fingers of the other groups. Average pre-immersion finger temperatures are shown in brackets. All tests were done under standard conditions.

HUMAN FACIAL RESPONSES

Subject group	No. of subjects	Energy state of subjects		Average finger temp. ($^{\circ}$ C)
		BMR (kcal/m ² /hr)	Rectal temp. ($^{\circ}$ C)	
Indian	6	42.20 \pm 1.60 *	36.80 \pm 0.10	8.74 \pm 0.77
Habituated	6	34.72 \pm 0.75	36.84 \pm 0.04	5.93 \pm 0.61
Control	6	35.35 \pm 1.04 **	36.77 \pm 0.10	3.45 \pm 0.77
Starvation	6	30.56 \pm 1.59	37.09 \pm 0.05	2.57 \pm 0.94

Significance of differences (P)

Indian vs. habituated	< 0.01	ns ***	< 0.05
Indian vs. control	< 0.01	ns	< 0.001
Indian vs. starvation	< 0.001	< 0.05	< 0.001
Habituated vs. control	ns	ns	< 0.05
Habituated vs. starvation	< 0.05	< 0.01	< 0.05
Control vs. starvation	< 0.05	< 0.05	ns

*Standard error

* *BMR was measured on only four of the control subjects

* * *Not significant (P > 0.05)

Table III. Relation between energy states of subjects and average temperatures of fingers immersed in 0^o C water for 10 minutes (under standard test conditions for all groups).

MILAN

previous 125 days. The averaged responses of the control fingers of this group were compared with the averages for the right middle fingers of each of the other groups. The average age for the habituated group was 27 years.

The Indian group consisted of six Alaskan natives from the Tetlin Reservation. They normally spent the greater part of the daylight hours out-of-doors, attending traplines, etc. These subjects were tested during the latter part of December, when it would be expected that they would have endured considerable recent cold exposure. At the time of this test, they had lived at the laboratory for one week under a regimen of restricted indoor activities. Their meals were taken entirely at the USAF Hospital cafeteria. During the week, they had been subjected to several oxygen consumption measurements and finger immersions in ice water, in connection with another study. Hence, they were accustomed both to the test and to the experimenter. Their average age was 23 years.

The control group consisted of six subjects who were engaged in indoor occupations and five of whom were employed at the laboratory. They were at ease with the experimenter but were not accustomed to the test. It was considered that they were comparable with the habituated group except for their unfamiliarity with the test. Their average age was 30 years.

The starvation group consisted of six subjects who were tested 1 or 2 days after returning from a regimen of starvation in the cold. They had lived for 5 days camped at individual sites on river ice, without food or sufficient thermal protection, in interior Alaska during the month of February. They were all accustomed to recent cold exposure and to the experimenter, and four of the six were accustomed to the test. Their average age was 27 years.

Every effort was made to have test conditions the same for the four groups. In all tests the compared fingers were immersed equal depths (2.8 ± 0.1 cm) in 0.0° C water for 10 minutes. The water bath was stirred equivalently in all tests. Temperature of

HUMAN RACIAL RESPONSES

the distal digital volar pads was measured using the one set of thermocouples which were always placed on comparable positions on the fingers.

Prior to tests the subjects slept overnight in a comfortable environment at the laboratory. Standard procedures were followed such that subjects were post-absorptive and normothermal at the time of tests. All tests were done between 0700 and 1000 hours in the morning. Oral and rectal temperatures were taken and basal oxygen consumption was measured while the subject remained in bed. Immediately after the subject arose from bed he was instrumented and with arms in the dependent position the middle fingers were immersed.

In all tests the estimated intensity of pain sensations from each immersed finger was recorded at each minute. (See pain intensity scale on Figure 4.) "Maximum pain" is the highest single estimate during the test, while "average pain" is the cumulative minute total divided by the time (10 minutes).

It must be emphasized that it is the responses of the control fingers of the test subjects (habituated group) that are compared with the responses of the right middle fingers of the other three groups. Figure 4 shows that in the capability for maintaining high finger temperature during ice water immersion the progression among the groups was Indian > habituated > control > starvation (although the difference between the control and starvation groups was not significant). The pain suffered by the habituated and control groups was roughly the same, while that of the starvation group was somewhat less, and in the Indians it was almost negligible. Thus there was no simple relationship between pain and finger temperature.

Table III shows the relation between the energy states of the subjects as they rested in bed just before the finger immersion test and the average finger temperatures maintained in the ice water. A direct relationship between metabolic rate and finger

temperature during immersion is strikingly demonstrated by the Indian and starvation groups. It is notable that rectal temperature is higher in the starvation group than in the others, therefore, finger temperature need not be related to the central thermal state. The most important results relevant to the assessment of local cold adaptation in vascular responses are shown in the comparisons of habituated and control groups. BMR and rectal temperature were the same for both. Yet the habituated group maintained a significantly higher average finger temperature ($P < 0.05$). Finger temperatures of the groups just before immersion were in the progression: Indian $>$ habituated = control $>$ starvation. The values in $^{\circ}\text{C}$ were, respectively, 35.2 ± 0.16 , 33.8 ± 0.28 , 33.7 ± 0.40 and 29.5 ± 1.53 . The mean finger temperature of the Indians was significantly higher than that of the others ($P < 0.05$) but the differences between the other means were not statistically significant.

General conclusions. It was shown that cold exposure of the human hand can cause a local vascular cold adaptation, or a marked, specific habituation to cold pain, according to the duration and intensity of the local cooling. Further, it was shown that a general habituation to the test procedure gives results which could be mistaken for a local vascular cold adaptation.

In conditions where man works outdoors in cold climates, it is likely that he will endure prolonged periods of moderate hand cooling and occasional periods of severe cooling. Hence, he might maintain higher finger temperatures through a vascular adaptation, and suffer less pain, even when finger temperatures were very low, through specific habituation. These adaptations, combined with a general habituation to the environment, could result in marked improvements in manual efficiency as the cold season progressed.

Yet another factor, which is incidental to these adaptations, may favor the maintenance of higher peripheral temperatures in outdoor workers. This is the higher basal metabolic rate which has been measured in Eskimos and northern Indians. Whether the higher BMR of these northern natives is mainly related to diet (Yoshimura et al., 1952*) or to genetic differences has not yet been resolved conclusively.

*Yoshimura, H., R. Iida, and H. Koishi. 1952. Studies on the reactivity of skin vessels to extreme cold. Part III. Effects of diets on the reactivity of skin vessels to cold. *Jap. J. Physiol.* 2:310-315.

THERMOREGULATION IN MAMMALS
FROM THE TROPICS AND FROM HIGH ALTITUDES*

Peter Morrison

The title presents something of a problem since there may well be no real entity "thermoregulation in tropical mammals" such as we see in other environments as the desert or the arctic which make special demands and have elicited special physiological capabilities. The tropics are distinguished in a negative rather than in a positive sense, by the lack of demands, at least of thermoregulatory demands, which are placed on the inhabitants. As has been pointed out, this region has a much better claim to the title of "temperate" than do our own middle latitude regions where extremes of temperature and rainfall are characteristic. But there are certain groups of animals which may be considered characteristic of these regions so that we can at least discuss thermoregulation in "some tropical mammals." However, these may well be characterized by a deficiency in regulatory ability rather than any special attributes for life there. The monotremes, and the edentates, might be considered in this category, but these groups have already been reviewed as primitive forms by Dr. Johansen. So I propose to survey first, the marsupials, then a primitive eutherian group, the Chiroptera, and finally the more advanced group of the Primates; all of which we can think of as characteristically tropical, although some representatives extend beyond this zone.

¹. *Much of the data discussed in this paper is as yet unpublished. Studies on Brazilian monkeys were carried out with J. Simoes, Jr.; on the pigmy marmosette with E. Middleton; on new world tropical bats with B. K. McNab, who also participated together with K. Kerst and W. H. Holthaus in the studies on high-altitude mammals. Support for these studies has been variously received from the Guggenheim Foundation, the U. S. Educational Foundation in Australia, NSF, NIH-PHS, WARF, ONR, and the Rockefeller Foundation.

Marsupialia

The marsupials have often been stigmatized as indifferent homeotherms usually because of the low reported level of the body temperature (T_B). But this conclusion suffers on three counts; first, a somewhat lower T_B is a poor criterion of homeothermism, we do not consider birds to be more homeothermic than mammals simply because they maintain a higher T_B ; second, a fairly limited assortment of marsupials has been studied; and third, since most marsupials are nocturnal, their study by diurnal physiologists has resulted in a falsely low estimate of their T_B level.

The first figure shows the relation between body temperature and ambient temperature (T_A) in a small American (brown) opossum (Didelphidae) in day and night. The diurnal values are quite distinct from the nocturnal ones, but both are accurately regulated (over a range) in response to cold. This relation (T_B vs T_A) describes the sum of regulatory activities with a horizontal curve representing complete regulation and one with a 45° slope (reference line), representing the absence of regulation seen in a poikilotherm. In addition to the slope, we must also consider the relation of the curve to the reference line since an animal may have a fairly labile T_B and yet maintain it well above the T_A . A third criterion of regulation is the variability of the T_B around the mean curve, but this may sometime provide a spurious index, since the scatter may only reflect a variation in the circumstances under which the measurements were made.

Figure 2 compares a rat-sized Australian representative (Dasyuridae) with an even more striking diurnal depression, near noon its T_B is about 34° C, but at night it is 38° C. Since the latter level is equivalent to that in the dog, Chaetocercus can hardly be considered defective or primitive in its level of regulation. But this is a form which can show a daily torpor. Another smaller relative (Antechinus) shows an even higher level during periods of activity (to 40°) although these periods do not follow a 24-hour cycle. Accordingly, it is necessary to identify any daily (or other) cycle and choose either or both, the maximum and minimum periods--the active and resting phases--to characterize the species.

ADAPTATIONS TO TROPICS AND ALTITUDES

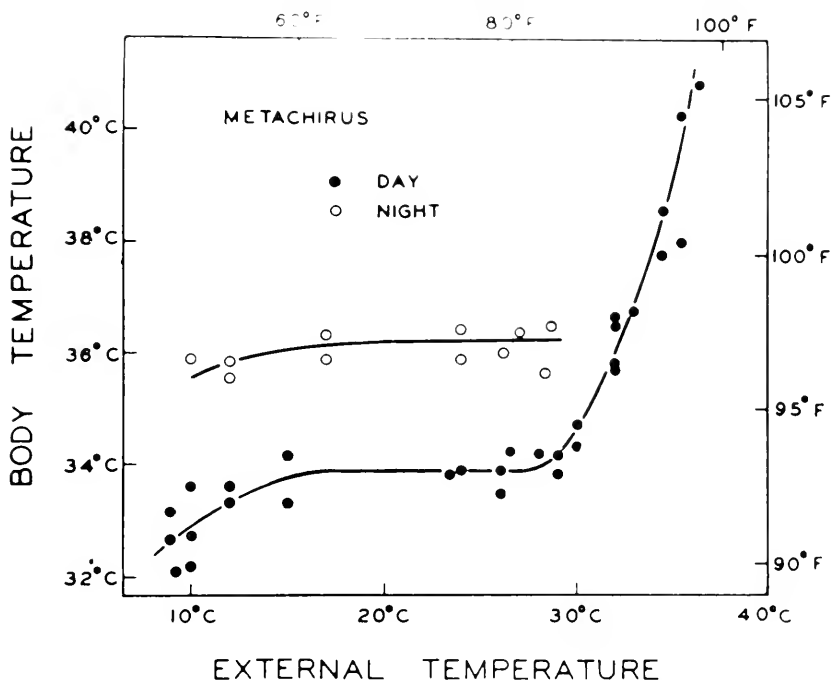


Figure 1. T_B as a function of T_A in the brown opossum (*Metachirus nudicaudatus*) showing the day-night difference.

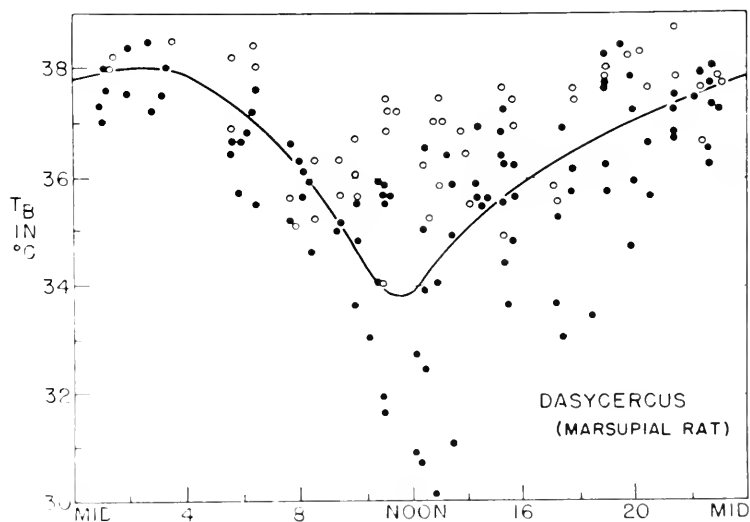


Figure 2. T_B in the Crest-tailed marsupial rat (*Dasyercus cristicauda*) as a function of hour of day.

Figure 3 represents an interesting form, the bilby. This is a desert representative of the small group of bandicoots (Peramelidae) which further emphasizes the independence in the day and night "settings" of the "thermostat." The daytime (inactive) T_B declined steadily through the course of the experiments, but time played no part in the level of the active temperature which stayed steady at 37° . These two states need not differ very much in activity but merely "wakefulness." The T_B after forced activity in the daytime never reached the natural nighttime level. Similarly, forced activity at night did not raise the T_B at all. So these are not passive noncommitants of extra heat production, but rather are maintained levels that are set by the animal.

Figure 4 recasts these data into a 24-hour cycle to bring out this very sharp nocturnal pattern. Like the brown opossum, the bilby regulates to a different level during day and night (Fig. 5). The bilby has excellent regulation to cold and this may seem contradictory since it is a desert species which comes from the Australian "center" where a high T_A is the rule. But the bilby shows no evaporative cooling and if put in a hot room at 40°C , elevates its T_B by $4\text{--}6^\circ\text{C}$ within an hour and must be removed to avoid heat death (Robinson and Morrison, 1957).

By contrast, Figure 6 shows another bandicoot with fair regulation to heat, with the T_B curve crossing the isothermal line to give T_B lower than the T_A . Of course, in terms of the slopes, what would be rather poor regulation to cold represents rather good regulation to heat, and yet this animal comes from the coastal regions, which are considerably wetter and cooler than the "center." So it is of interest that a desert animal need not be characterized by the ability to maintain itself under desert conditions, while an animal from a less rigorous environment can do better. The answer, of course, is in the stringent requirements of desert life, such that the bilby must always use microclimatic evasion to avoid the expenditure of water.

The short-nosed bandicoot showed an interesting feature in relation to the topic of seasonal modification discussed by Dr. Hart. These animals always showed good "cold" regulation at night (Fig. 6), and in the winter they regulated well during the day or night.

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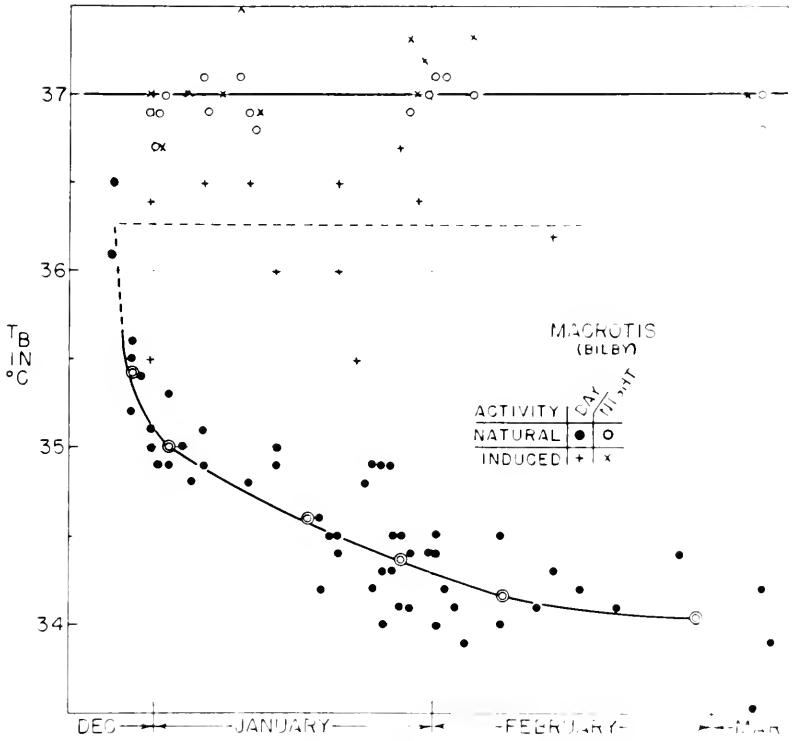


Figure 3. T_B in the rabbit bandicoot or bilby (Macrotus lagotus) during continued captivity.

MORRISON

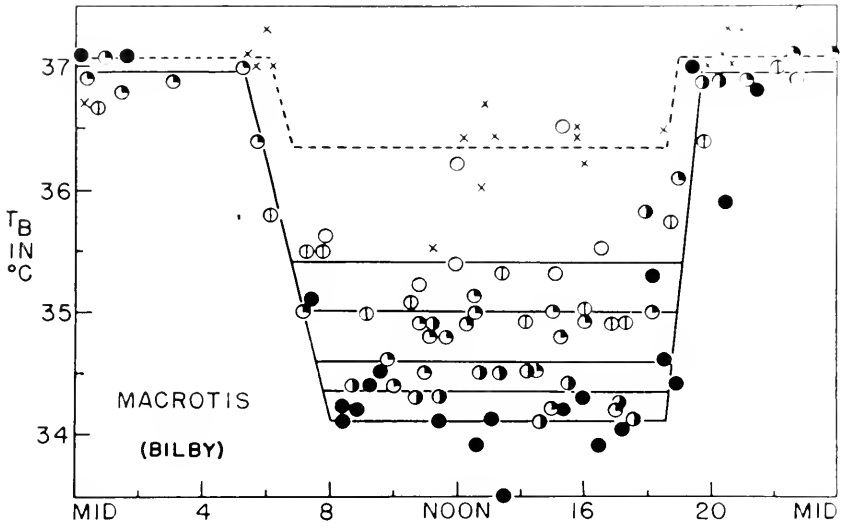
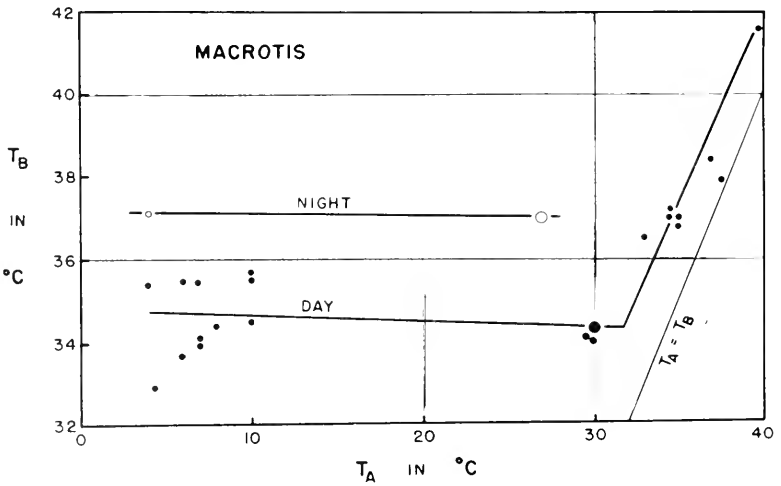


Figure 4. Daily T_B cycle in the bilby (*Macrotus lagotis*). Different symbols show successive periods of time.



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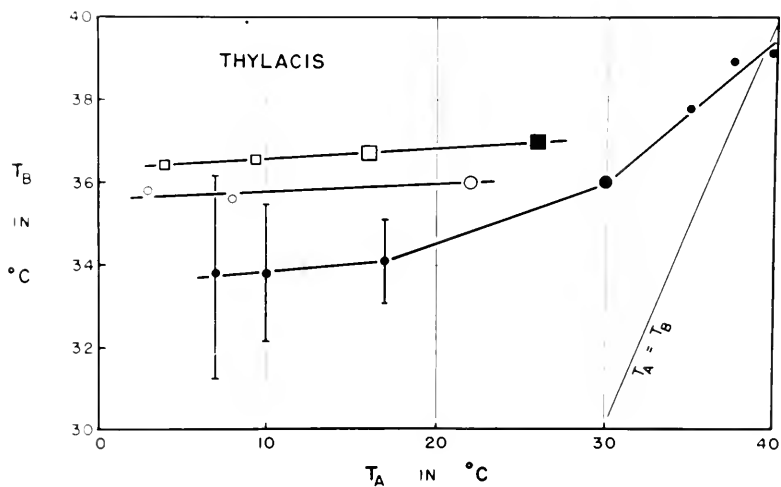


Figure 6. T_B as a function of T_A in the short-nosed bandicoot (*Thylacis obesulus*). Open symbols, winter; closed symbols, summer; circles, day; squares, night.

But the summer animals did not maintain their temperature in the daytime. So this suggests that there is some kind of adaptation of thermoregulatory control not in the metabolic capacity nor in the insulation, but in the ability to respond to a stimulus which it may not encounter.

Figure 7 describes the koala. This is a familiar sluggish marsupial (Phalangeridae) which has poor temperature regulation to cold as can be seen from the very substantial slope to the T_B curve. In this regard the koala seems quite inadequate, but since the T_B curve continues almost in a straight line across the isothermal line, it actually has quite effective regulation to heat; much better, indeed, than many of our higher mammals, such as the rodents, which cannot maintain the T_B below the T_A . There is again a considerable scatter in these points, but much of this could be eliminated by proper definitions of the conditions. This is a particular problem with a sluggish animal which adjusts only slowly to new circumstances. As one might expect, the afternoon T_A is warmer than the morning T_A . But this is a diurnal animal and so part of this slope of the T_B curve reflects the daytime activity.

The examples given thus far might tempt us to characterize the marsupials as animals with very large diurnal cycles, and even to represent a measure of thermal instability, although this is a matter of some argument. But Figure 8 shows, for contrast, a small wallaby (Macropodidae) with no daily cycle at all. Similarly, Figure 9 presents one of the larger macropods in which the diurnal cycle is again absent. But in part this effect is spurious as a representation of the animal in nature because an animal as large as the kangaroo is not able to engage in his normal activity when maintained in close captivity. If it is normally occupied with moving and feeding, higher nocturnal values are obtained. However, Figure 9 is principally of interest in illustrating or suggesting another phenomenon. The checkered circles averaged by the upper dotted curve represent T_B values that were taken during the week following a critical heat test in which the animal was exposed for 6 hours at 40° . During this exposure the T_B was not markedly elevated (only to 35.4° C), since kangaroos are excellent regulators to heat. Nevertheless, following this heat exposure, an elevated

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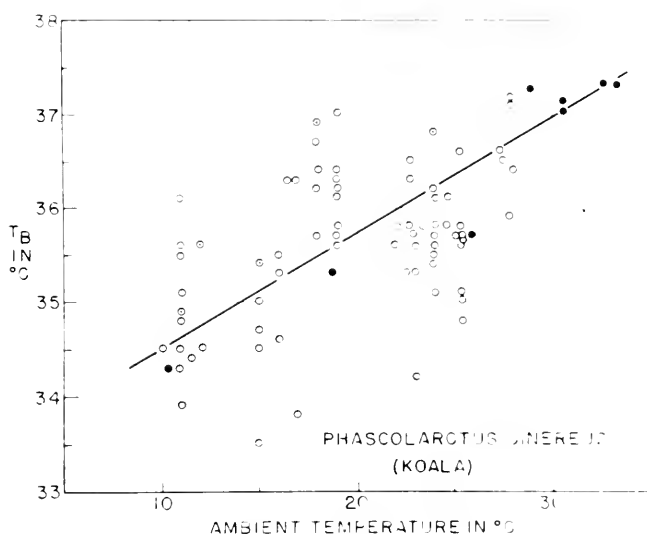


Figure 7. T_B as a function of T_A in the koala (Phascolarctus cinereus).

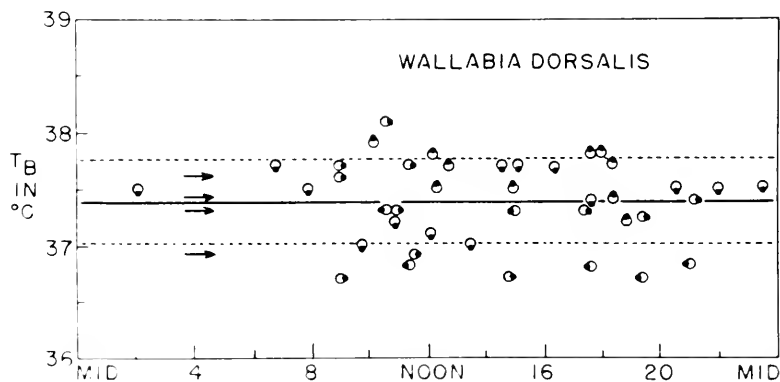


Figure 8. Daily T_B response in the black-striped wallaby (Protemnodon [=Wallabia] dorsalis). Individuals differentiated by symbols.

T_B was recorded, not only on the following day, but for more than a whole week thereafter. The crossed circles in Figure 9 represent the second week after that exposure with some return towards the normal level, and then finally the lined circles show the return to normal in the third week. Here, then, is a suggestion of an adaptation of T_B in response to a thermal stimulus, a response which as Scholander et al. (1950) point out is not appropriate to cold. But because a difference of only a degree or two in T_B in a hot climate may allow the elimination of evaporative cooling, it could be a very useful response to heat.

In summary, the marsupials are a primitive group which cannot be characterized by a single thermoregulatory pattern. Some show excellent regulation to cold while others are cold-sensitive. Some have very effective regulation to heat while others have none. There does seem to be some disposition towards thermal lability, although not necessarily thermal inadequacy in the group.

Chiroptera

The Chiroptera have always been of special interest because of the seasonal and daily hypothermia exhibited by those temperate forms which have been studied. However, they are essentially a tropical and subtropical group, so we should, perhaps, characterize the order in terms of the tropical representatives. It is in the tropics that they show their greatest profusion, both in numbers and in their specializations for different environmental or behavioral situations. The flying foxes, or Megachiroptera, weigh as much as a kilo and are very substantial animals. In Australia we found that one megachiropteran (Pteropus) regulated its temperature very well against cold, and that it had insulative properties and metabolic responses which were quite comparable to small temperate-zone mammals of the same size (Morrison, 1959). We were, therefore, interested in Brazil last year to examine a series of the microchiropteran fruit bats, largely from the Phyllostomidae.

Figure 10 shows the daily cycle for one of these genera, Artibeus. The cycle is substantial, but not extreme, with a range of about 3° C between the mean minimum and maximum levels.

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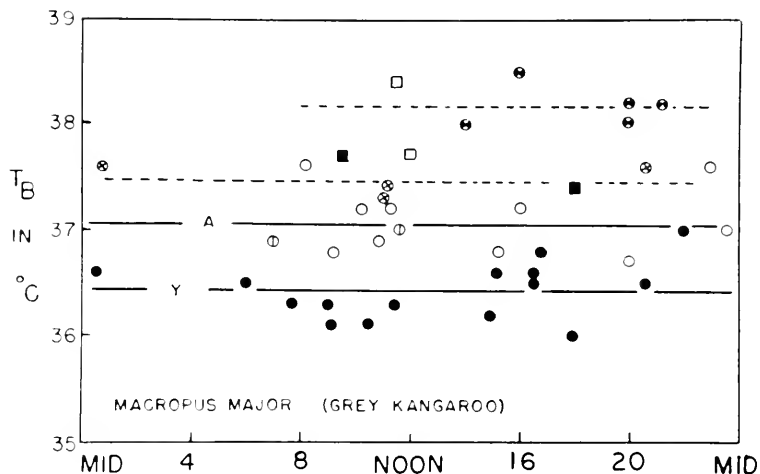


Figure 9. Daily T_B response in the grey kangaroo (Macropus major). Closed circles show ordinary temperature in a young animal; open circles in an adult; squares represent active animals; other symbols follow heat exposure (See text).

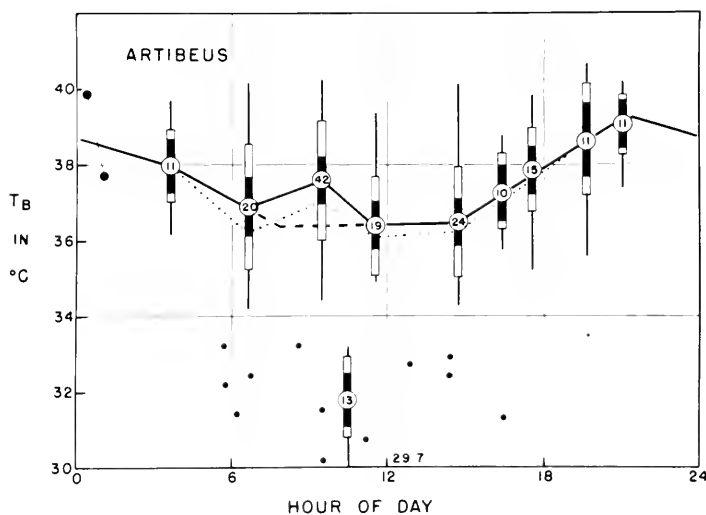


Figure 10. The daily T_B cycle in Artibeus. Symbols show sample size, mean value, 2 x standard error, standard deviation and range.

A small scattering of points below the main body have not been included in the heavy average because they represent a distinct population, but their inclusion as shown by the dotted curve does not change the picture appreciably. Figure 11 presents the thermoregulatory response to cold in this species and shows it to be an adequate regulator since the slope is a modest one, comparable to that in many other mammals. Under heat stress, however, there is almost no regulation, the slope being little less than the value of 1.0 characteristic of a poikilotherm.

Figure 12 shows a somewhat different T_B response in a smaller species. At modest T_A values of 15-20° C, the T_B falls substantially. But when the T_A is cooled further, the animal seizes hold and regulates its temperature quite effectively. Thus, the reduced T_B did not represent a deficit in capacity or ability to regulate, since the animal regulated well at an even lower T_A . It can be considered as representing a kind of deficiency--careless thermo-regulation--but there may be functional implications. This type of response may be seen in other mammals. The jumping mouse (Zapus), for example, may cool appreciably at intermediate T_A values, but regulates well at or below 0°. Again, there is no deficit in the capacity or ability to regulate, but the animal retains an option as to its use.

Figure 13 shows the daily cycle in a larger bat (Phyllostomus) which differs somewhat. The two peaks are characteristic of a crepuscular animal which feeds at dawn and dusk. Again, there are a number of points which exceed the dispersion of the bulk of the values (d 3 S. D.), and we have in addition some very low points which approach the T_A . This polydispersity (seen also in Artibeus, Fig. 10) suggests that we may be dealing with several conditions or activity levels, a situation already indicated in the insectivorous bat Miniopterus (Morrison, 1959). This suggestion appears to be confirmed in Figure 14 which shows the more complicated response of Phyllostomus to cold. Now in Figure 13 this bat could be thought of as operating under different conditions--perhaps "active," "quiet," "sleeping" and "torpid." It was ordinarily resting during the daytime but even then could become active with a higher T_B . Occasionally it showed a torpid, poikilothermic

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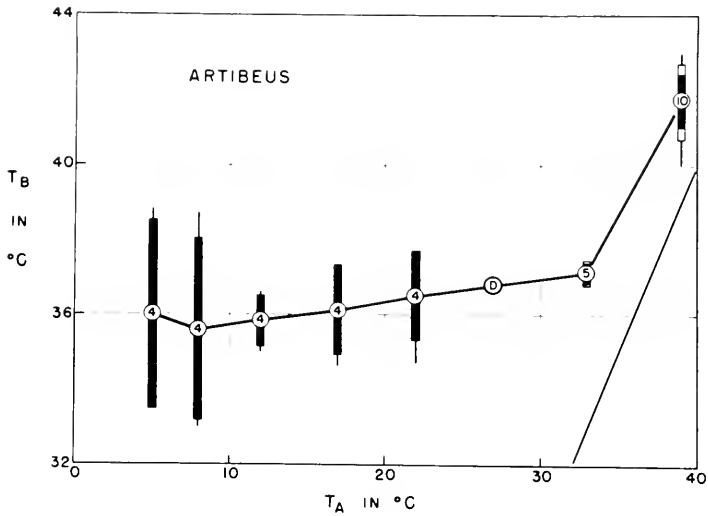


Figure 11. T_B as a function of T_A in Artibeus.

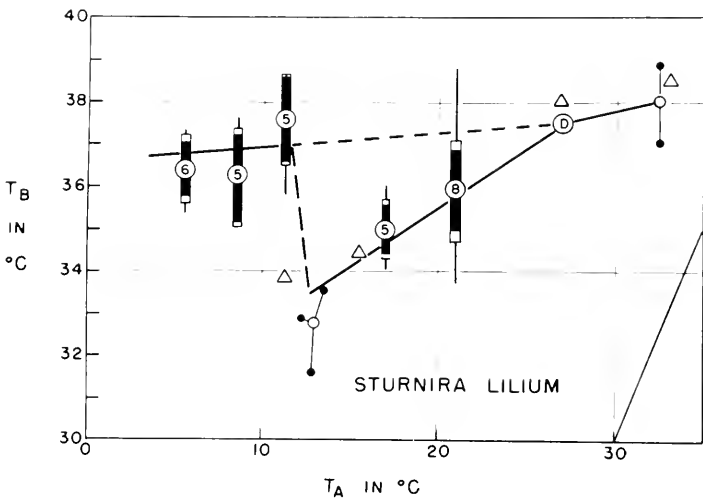


Figure 12. T_B as a function of T_A in Sturnira. Triangles represent another species (Vampyrops) which conforms to the same pattern.

MORRISON

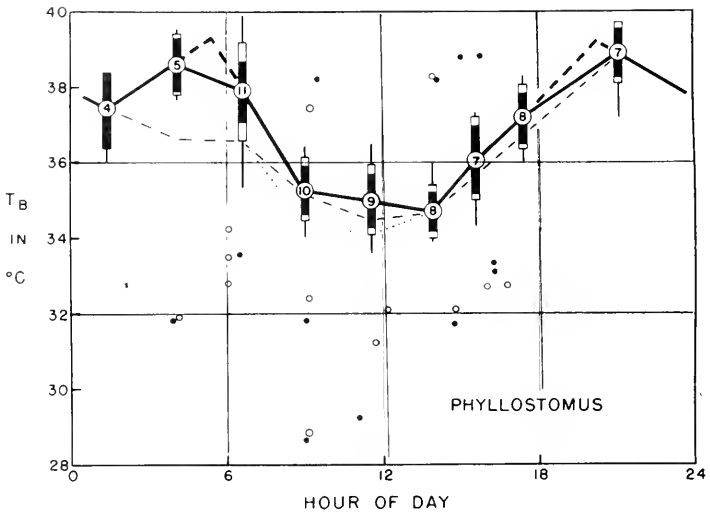


Figure 13. Daily T_B cycle in Phyllostomus.

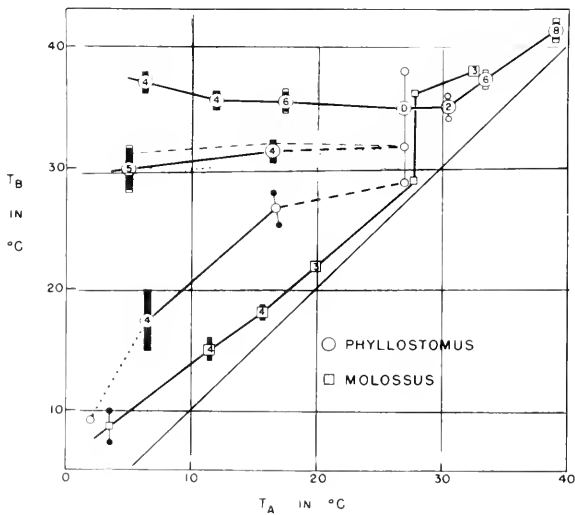


Figure 14. T_B as a function of T_A in Phyllostomus (circles) and in Molossus (squares).

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state where the T_B approached the T_A . Also in bats here, as in *Miniopterus*, there can be an intermediate zone (sleeping?)--not poikilothermic in the ordinary sense, but just a little above 30°C where the animal can become active rather quickly, but still effect an appreciable metabolic savings. Now, the T_B groups in the cold exposed animals can be associated with these groups, although they may not be exact projections. The upper curve (Fig. 14) maintains the "resting" level and at 6°C ambient, as a more vigorous metabolic response is required, even approaches the "active" level. The intermediate curve with T_B values near 30° maintained even at 6°C ambient, gives further credence to the concept of a maintained "sleeping" level. Finally a few much lower values (lower curve) would represent torpor although not as low as the ambient level.

Figure 14 also compares Molossus, a tropical insectivorous bat, which uniformly became torpid when exposed to cold, although not quite to the degree expected of a similar temperate bat. Figure 15 shows the daily T_B cycle in this species (lower curve) which also closely resembles the behavior of our northern bats with elevated activity at dusk and dawn and torpor during the day. Eisentraut (1950) has discussed tropical insectivorous bats which he found to have a broader "range of activity temperature" than their temperate relatives and thus not ordinarily to enter into a state of torpor during the day. This was certainly the case in the situations where Molossus was collected ($T_A = 30^\circ + \text{C}$) but in the laboratory at a T_A of 26°C to 28°C it certainly entered torpor.

In Figure 15, also, the curves for the 4 frugivorous bats are compared. This set of curves presents an interesting sequence of parameters in order of decreasing animal weight. Thus, in this series, both the resting diurnal and the active nocturnal levels are increasing, the rate of change between the two activity states is decreasing, and the diurnal fall is postponed, although the nocturnal rise is fairly synchronous for the several species. The insectivorous Molossus fits into these sequences in all regards except weight, since it is the smallest of the lot. It is not now possible to interpret these systematic regularities, but they no doubt fit into some general pattern of thermoregulatory properties.

MORRISON

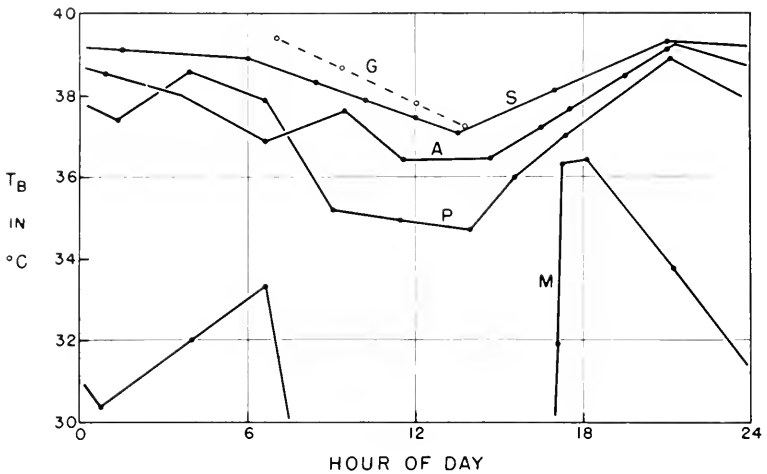


Figure 15. Summary of daily cycles in different species of bats: M, Molossus; P, Phyllostomus; A, Artibeus; S, Sturnira; G, Glossophoga.

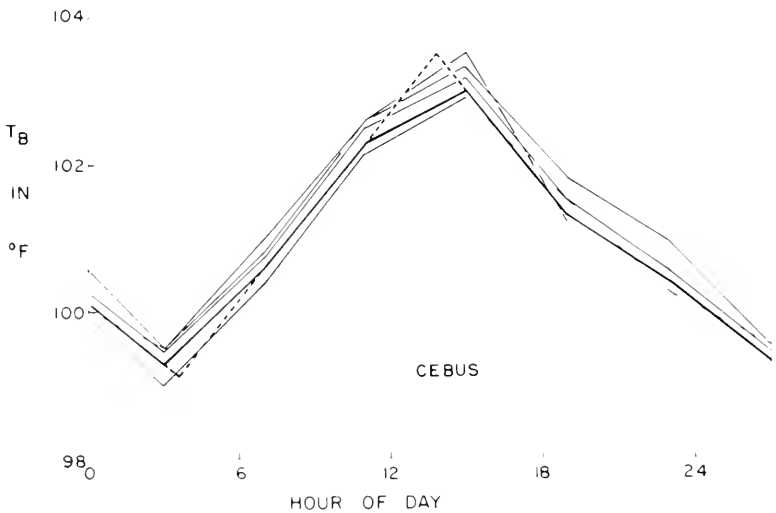


Figure 16. Daily T_B response in four species of Cebus to illustrate conformity of pattern. Points on mean curve (heavy) represent some 350 values. Data from Dr. H. L. Ratcliffe, Penrose Research Laboratory.

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In summary, the chiroptera also show a variety of responses. Traditionally the insectivorous species are characterized by their thermolability, but the behavior of some of the frugivorous species can be indistinguishable from other mammals. However, even in the larger bats scattered values suggest a latent thermolability which may be manifested under appropriate conditions. But since this thermolability, either expressed or latent, appears to be suited to the environmental and metabolic needs, we should hesitate to describe it as a primitive feature or an inadequacy.

Primates

The last group to be considered is an advanced one, but with one exception, is even more strictly limited to the tropics. There is considerable T_B data on the Primates partly because of their use as laboratory animals, but also because of tuberculin testing, particularly at the Philadelphia Zoological Garden, (Brown, 1909; Fox, 1923). Some recent data are shown in Figure 16 which compare four species of Cebus and shows the extreme regularity of their response. The temperature cycle with an amplitude of 2.5°C is substantial, but not extreme.

Figure 17 represents a smaller primate, the marmoset (Callithrix), which shows a striking diurnal cycle with an amplitude of almost 4.0°C . Although these animals adapt well to handling and have been popular as pets for more than a century, there is almost no physiological information on them. Figure 18 considers another marmoset which is of interest as the smallest of the primates and weighs about 100 g. It, too, has a very striking cycle, although not so large as Callithrix. A unique feature is the minimum, which is very low for a primate. One may wonder if the cryptorchid condition sometimes reported in this genus (Hill, 1959) depends on this low body temperature, in accordance with the general relation between body temperature and descent of the testes as discussed by Wislocki (1933). Figure 19 shows the effect of limiting temperature measurements to six fixed times during the day as has been done in many measurements on Primates. A substantial distortion results with a plurring of the almost "square" wave form seen in Cebuella and a loss of resolution of secondary waves.

MORRISON

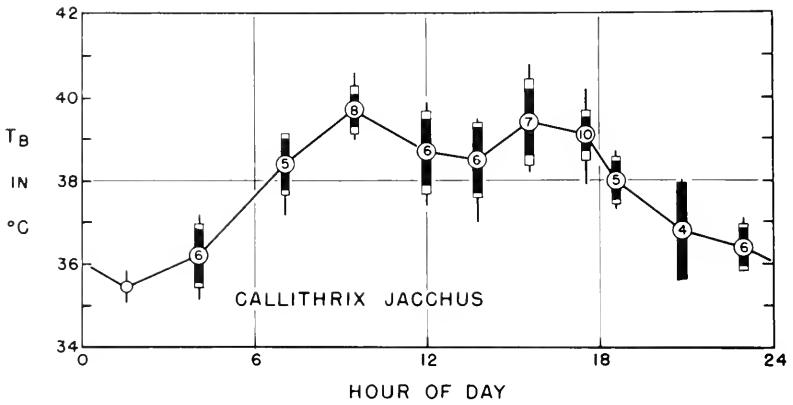


Figure 17. Daily body temperature response in the common marmoset (*Callithrix jacchus*).

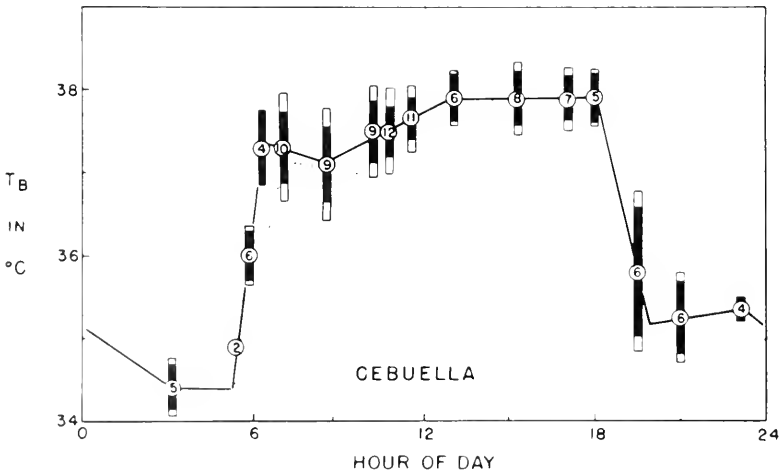


Figure 18. Daily temperature response in the pygmy marmoset (*Cebuella pygmea*). Dashed curve shows same curve inverted and displaced by 12 hours to illustrate cycle symmetry.

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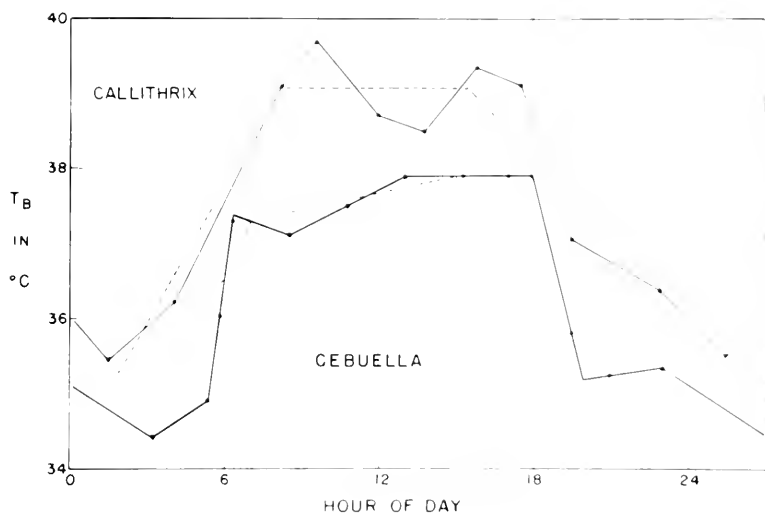


Figure 19. Distortion of the daily cycle of the use of fixed time points (03, 07, 11, 15, 19 and 23 hr.).

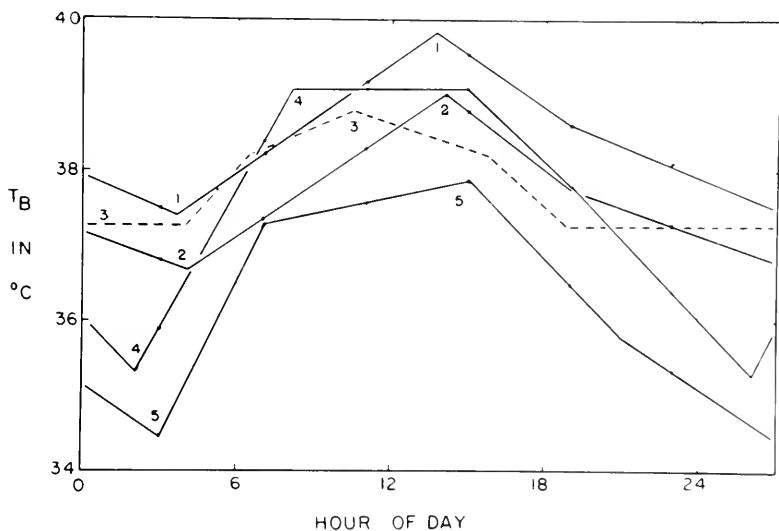


Figure 20. Comparison of daily temperature cycles in new world monkeys: 1, Cebus; 2, Ateles; 3, Aotus; 4, Callithrix; 5, Cebuella. Broken curve for the nocturnal Aotus has been shifted twelve hours to allow comparison to diurnal forms.

Figure 20 compares the form of the daily cycle in several of these new world monkeys. Although at a lower level, the form of the curve in Ateles is strikingly similar to that of Cebus. By contrast, curves of the two marmosets, representing the more primitive Callithricidae, are quite distinct. Also shown in Figure 20 is the night monkey (Aotus) whose cycle, however, has been shifted by 12 hours so that it could be compared to the others. Nocturnal forms are rare among the primates and the limited amplitude of this nocturnal cycle suggests that the daily cycle may not be merely a casual concomitant of the time of activity, but be more formally impressed into the "matrix" of the animal. Thus, in this instance, the nocturnal Aotus has reversed the characteristic primate diurnal cycle, but has achieved only a limited amplitude.

Figure 21 compares another aspect of regulation in two of these species to show that while Aotus has excellent "cold" regulation, Callithrix is quite sensitive to cold. A correlation might be made with the nocturnal habit, but it is only fair to note that Aotus ranges up the Andean slopes to fairly cool situations. The response of the smallest primate (Cebuella) to cold is shown in Figure 22 and shows even less resistance to cold than the larger Callithrix. But its resistance to heat stress is distinctly superior, and at a T_A of 40°C it maintains a T_B of 40°C .

Figure 23 shows the metabolic response of Cebuella at varying T_A and presents a good example of the problem of fitting a conductance value to a thermolabile animal. If we describe our homeotherm in terms of the simplest model then the heat flow or metabolism will be proportional to the temperature differential (Scholander et al., 1950a). But, as was seen in Figure 22, the maintenance range for T_B in Cebuella was only between 15°C and 30°C , and below this we will find reduced T_B and metabolism. Accordingly, if the metabolism is plotted directly against T_A the mean curve will have too low a slope (low conductance) and will extrapolate above the T_B . To adjust for this error, the metabolism may be plotted against the temperature differential, $T_B - T_A$ (top scale in Fig. 23); or to maintain a more familiar scale, the T_A may be corrected by the amount of the T_B depression (bottom scale in Fig. 22). With this procedure, a good linear representation is obtained with extrapolation to the T_B (38°C) at the abscissa. The conductance curves

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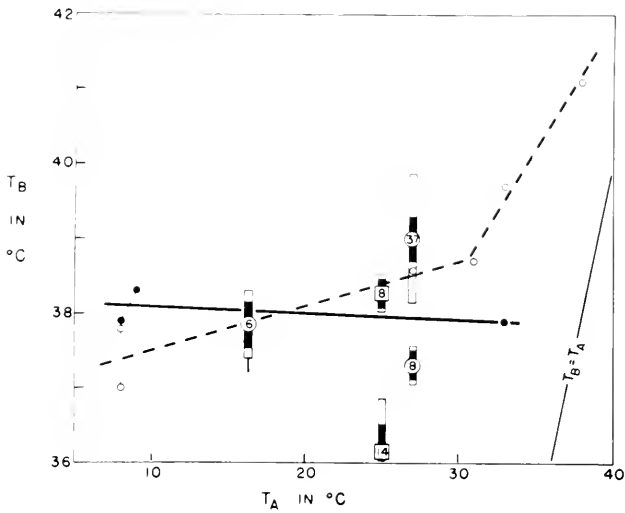


Figure 21. Body temperature as a function of ambient temperature in *Callithrix* (open symbols) and *Aotus* (closed symbols). Squares represent night values; circles are day values.

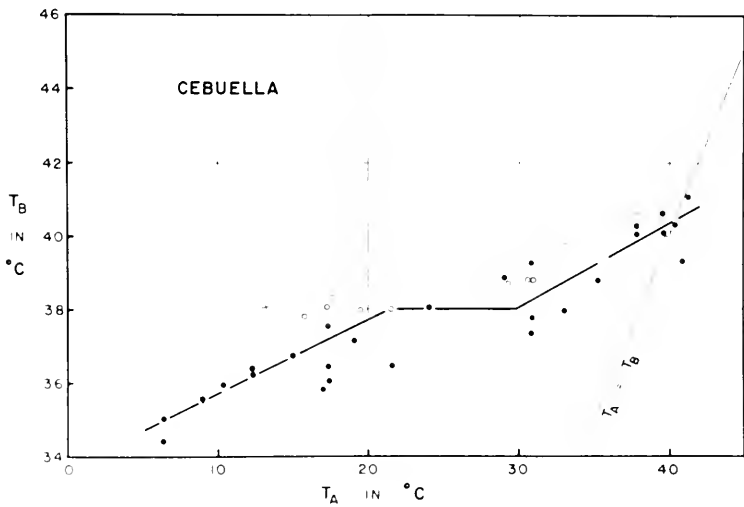


Figure 22. T_B in *Cebuella pygmaea* as a function of T_A . Open symbols, male; closed symbols, female.

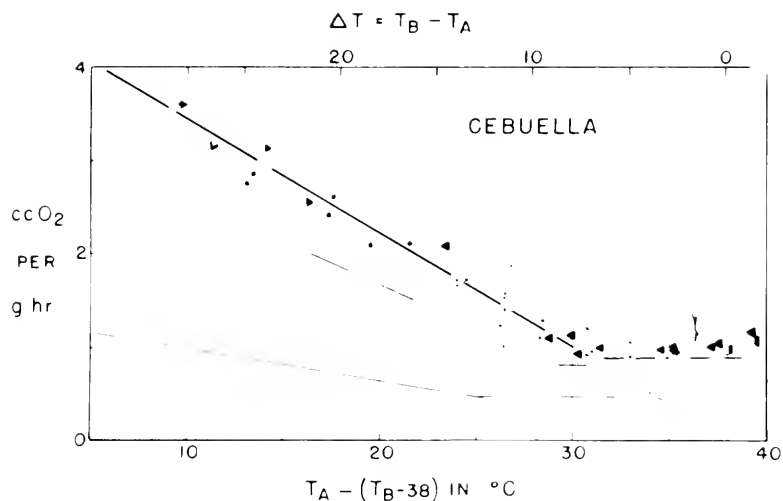


Figure 23. Metabolism as a function of ambient temperature in the pygmy marmoset. Triangles represent points adjusted for fall or rise in body temperature. Large points represent standard body temperature (38.0°). Small symbols, no temperature measurements. Light curves compare metabolic response in Aotus (lower) and Callithrix (upper).

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for the other two primates are also compared in Figure 21. Most of the observed differences relate to the differences in size. The values for the two marmosetts lie just above the mean curve relating conductance to body weight in some temperate small mammals, $C = W^{1/2}$ (Morrison and Ryser, 1951). Aotus, by virtue of its more effective insulation, has a conductance appreciably below the mean curve.

In summary, this limited survey of thermoregulation in the primates has again shown some regularities in the daily cycles, but also some variety in this and in the response to cold. Also, to consider again the general question as to common thermoregulatory features shared by tropical mammals, there appears to be none. Certainly there is great variation in the maintained levels both diurnal and nocturnal. The response to cold and as well, to heat, appear equally variable since either or both may be present or absent. Even the criterion of inferior insulation cited by Scholander et al., (1950) does not hold for many of the smaller tropical species. Indeed, perhaps we can only characterize the tropical mammals by the complete heterogeneity of the thermoregulatory responses.

Altitude and Thermoregulation

The relation between thermoregulation and altitude appears even more tenuous than that of the tropics. It is true that if oxygen is sufficiently withheld from a mammal in the cold, its T_B will fall (Nielsen et al., 1941). But other functions and activities will be similarly impaired. Of course, to the extent that thermoregulation may require a considerably greater energy output than other functions, it will be preferentially affected--and also, as a regulation that is, perhaps, less critical than some others, it might be preferentially dispensed with as in the camel (Schmidt-Nielsen et al., 1957).

We have recently investigated the altitudinal responses of a number of Andean rodents, and the matter of their transport capacity for O_2 at varying altitudes bears on the present point since it represents a limit for energy output. Indeed, our experimental

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procedure involved a cold stress (at 5° C to 10° C) to raise the metabolic level. The oxygen tension was then lowered in successive steps until a reduction in oxygen consumption was observed. This was always followed by more or less severe hypothermia depending on the duration of the experiment.

As an index of performance, we choose the pO_2 at which the metabolism was reduced to twice the basal level.² Of our "low" species, the least effective was the Chilean degu (Octodon degu), a rat-sized, histricomorph rodent. The "critical" pressure for the degu was sometimes reached at an pO_2 of 110-120 mm, a reduction of only 1/4 from that at sea level. The other extreme was seen in one of the species of the high-altitude genus of Akodon, a small cricetid rodent, which could still be effective at a pO_2 of 50-60 mm, or about a third that at sea level. These were the extremes, and although animals from high altitude were on the whole much more effective than animals from sea level, a spectrum of "critical" pressures was seen. Thus, the best "low" species (Oryzomys l. longicaudatus) was more effective than several of the "high" species. The differential performance of different species from the same environment appeared to relate to general "fitness" or "athletic development." Thus, the Oryzomys was markedly the most vigorous of the low species, and it is quite reasonable that their greater metabolic potential will also be effective under the handicap of hypoxia. In a similar manner, wild guinea pigs showed significantly greater performance than their more sedentary domestic relatives taken from the same altitude.

In summary, Andean rodents from high altitude do show superior thermoregulation to cold stress when measured at low oxygen pressures. This facility appears to be unrelated to the moderate increase in cold stress on the altiplano, and relates rather to the general improvement in transport capacity by which the species adapt to the requirements of their hypoxic environment.

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DISCUSSION

HUDSON: Dr. Morrison, do any of your studies correlate these tolerances of the oxygen tension within the aspect of the cardiovascular system? In the case of the house mouse you mentioned the lung and the diaphragms, so I suppose that answers part of my question.

MORRISON: Our primary objective was an evaluation of overall performance, but we examined a number of details. For example, the hemoglobin level in native mice at high altitude appears no greater than at sea level; but at both levels, hematocrits are higher in the "vigorous" species as compared to "less vigorous" species. We were not prepared to examine the factor which I suspect is the most significant, namely the capillary discharge of oxygen. Because there were only modest changes in the other factors in the chain--lung and heart size, heart and respiration rates, hemoglobin level, etc.--we are forced to conclude that there is some specialization, perhaps an increase in number, or a lengthening and contorting, of the capillaries. This would really be an optimal adaptation with minimal distortion of the normal pattern of the animal; and it would seem that this normal pattern is rather important. The house mouse does adapt, but I am sure that he is at a concomitant disadvantage in some way because it has distorted the normal mammalian form (i.e., lung fraction, heart fraction, hematocrit, etc.) which is a very constant feature. I cannot say just why the normal proportions are optimal, but I think it must be so.

Of course, you human physiologists know the problems of getting comparable material. I was impressed by this in Peru where some studies compared miners from Ororococha to other subjects from Lima. Some miners had more work capacity at 15,000 feet than the urbanites had at sea level, but clearly the development and conditioning of these subjects differed by much more than altitude.

HART: May I ask Dr. Morrison a question about the study of mice at high altitude? Were they all small mammals in your high altitude and low temperature comparison?

MORRISON

MORRISON: Yes, up to the size of a rabbit.

HART: Are these all good regulators?

MORRISON: We did not do exhaustive studies of regulation, but they seemed to regulate well.

HART: With five degrees of cooling do they always double the heat product?

MORRISON: Yes, for all the mice and rats. And incidentally, in a regime like this it is desirable to have knowledge of "where you are going," so that the cold exposure is not too prolonged. Knowing the animal and the previous experience one can approach the critical oxygen pressure quickly.

HART: Your critical temperature was quite high in all of them, I gather from this.

MORRISON: Yes, it was in relation to their size and insulation.

PROSSER: Did you find any differences between the sea level and the altitude population of the *Phylotus*?

MORRISON: By this index, yes, very definitely.

PROSSER: Is there any evidence that this is genetic?

MORRISON: Yes. We took high-altitude mice to sea level. They bred there and bore the litters which were raised to adults. The performance of these "low-raised" mice approached that of the parents. They had spent their entire lives at sea level and yet they were physiologically high-altitude mice.

JOHANSEN: In your many curves of the body temperature plotted against ambient temperature, it seems inevitable to me that the curve must bear some relation to the time of exposure to these temperatures, particularly below the critical temperature for the species.

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MORRISON: No, these were not, in general, situations in which the body temperature was falling progressively. And, in fact, in many instances in comparing a 1- to a 2-hour or a 2- to a 4-hour exposure, the second body temperature would be higher than the first. These are essentially maintenance temperatures.

EAGAN: Did most of your measurements consist of several measurements on one animal in order to arrive at the statistics, or a single measure of the single animal?

MORRISON: Measurements of several animals; but not in all cases. This is one aspect of comparative physiology in which one cannot be too fancy in experimental design because the most important point of departure is to catch an animal. The work on the very interesting bilby represented a single individual. I do not like to work on a single individual any more than the rest of you, since it imposes limitations, but it is amazing what can be found out from a single specimen if it is husbanded.

EAGAN: Do you lump the data all together then, or do you average them for animals under the same conditions?

MORRISON: Well, we do both essentially. Usually the data are plotted with individuals identified to see whether there are different patterns of response. If none is seen, the data is then grouped and averaged without respect to the individual. In the "triple response" of the bat Phyllostomus to cold there were some definite correlations such that one individual always gave high values while two others always gave low values.

IRVING: Would it be anything more than a scheme for trying to organize some of the information in my memory to think that their very interesting elevation of the metabolic rate after its decline in moderate conditions, when the animal was further cooled resembles the response that one sees in bats and arctic ground squirrels? Do you recall that bats and arctic ground squirrels do awaken from hibernation if the body temperature is cooled below a certain level; some of the hibernators will reawaken and begin to generate heat actively. Do you think this phenomenon of yours is perhaps another phase of the same sort of thing?

MORRISON

MORRISON: Exactly. Operationally, it is just the same kind of situation. In the ground squirrel, the thermogenesis seems to act as an alarm system rather than a thermostat. If its body temperature drifts down below a fixed point, near freezing, it awakens and normal body temperature is maintained thereafter. These bats act in the same manner except that the alarm is set for 30° C to 33° C.

JOHANSEN: We saw exactly the same thing in the birchmouse, Sicista betulina, in regard to these diurnal variations. If you force on them a large negative heat load their body temperatures rise quickly.

IRVING: Or you can say the same thing then, perhaps with reference to the excellent discussion of the torpidity in birds. At the small power output it is possible that the cold metabolic animal could not tolerate very low temperatures.

MORRISON: Torpidity is incompatible with temperatures below freezing.

IRVING: Yes, they either have to reawaken or die.

MORRISON: I do not know whether they would be able to or not.

IRVING: Do you think birds can be reawakened from torpidity by excessive lowering of temperature?

MORRISON: Yes, very definitely.

IRVING: I was just wondering how you would compare them with the faculty which you have shown to be so rather widespread in mammals. I have not seen it mentioned. That is why I inquired.

MORRISON: It would be well worth looking into, particularly in some of the Californian species.

IRVING: It is always stuck in my crop that there is something that distinguishes torpidity in birds but it may be only in the way that people have looked at it.

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HANNON: As yet, we have not had any comment on temperature regulation in the shrew. Dr. Morrison's name has long been associated with shrew metabolism. Would you care to comment on the temperature regulation of these animals?

MORRISON: I think all one can say is that temperature regulation represents an adjustment so that heat output equals heat production, and that these animals are obviously so adjusted. They do not really have a problem because of their high metabolic rate; obviously the heat flux from these animals per gram of tissue is very great.

HANNON: Have you ever studied the metabolic response of shrews when they are exposed to different temperatures? Have you ever determined the lower temperature limit for the maintenance of homeothermy?

MORRISON: You mean to exceed their limit of regulation.

HANNON: Yes.

MORRISON: Yes, we have done that, and our Sorex from Wisconsin could not take more cold than -10° to -15° depending on the wind. We used this limit to estimate the maximum metabolic rate; the value was close to that which we observed for short periods of sporadic activity. But we did not run them on a treadmill.

TEMPERATURE REGULATION IN DESERT BIRDS AND MAMMALS

Jack W. Hudson

Birds and mammals living in deserts utilize a variety of physiological, morphological, and behavioral patterns for coping with their environments. Although any pattern is adaptive when it allows a species to live and reproduce successfully in its habitat, there are examples of desert species which illustrate unique physiological mechanisms for coping with high temperatures and limited availability of water. For example, the camel (Camelus dromadarius) shows striking thermoregulatory adaptations to high temperatures and limited water supplies (Schmidt-Nielsen et al., 1957) and the kangaroo rat (Dipodomys merriami) demonstrates an excellent capacity to conserve water (Schmidt-Nielsen et al., 1948a, 1948b). However, some species of birds and mammals are able to occupy the desert habitat even though they have no unique thermoregulatory capabilities or special abilities to conserve water. For example, the wood rat (Neotoma lepida) has no unique thermoregulatory ability, and it has only a modest capacity to conserve water, a capacity approximately equivalent to that of the Norway rat (Lee, 1960). Likewise, the House Finch (Carpodacus mexicanus) and the Mourning Dove (Zenaidura macrura), which may live in the desert, have no special ability to minimize water requirements (Bartholomew and Cade, 1956; Bartholomew and MacMillen, 1960), while the Abert Towhee (Pipilo aberti) does not possess any capacity for temperature regulation absent in other passerines (Dawson, 1955). Furthermore, neither the House Finch nor the Mourning Dove is able to process salt solutions as concentrated as might be expected if its kidney were well adapted for the conservation of water (Bartholomew and Cade, 1956, 1958, 1959; Bartholomew and MacMillen, 1960).

There are many ways birds and mammals can avoid the environ-

mental extremes of high temperature and limited availability of moisture characteristic of the desert. Among these are nocturnality, fossorial habits, aestivation and hibernation, and dependence on succulent foods. The many "niches" available are correlated with a variety of successful adaptive patterns found in desert birds and mammals. It is not surprising then, that a broad spectrum of physiological abilities for coping with high temperatures and limited availability of water is found among desert inhabitants. A species possessing physiological mechanisms meriting a subjective judgment of "well adapted to the desert environment" is one which occupies a "niche" where high temperatures and a limited availability of moisture must be contended with. The converse would be true of "poorly adapted" species.

The difficulty of precisely describing the niche of a small bird or mammal has been the subject of much discussion among biologists. However, some insight into the delineation of the "niche" may be acquired by examining the physiological performance of a species in the laboratory as an index of the environmental parameters to which it is adapted. From observation of the variety of adaptive mechanisms so far found in mammals of the deserts, it is becoming apparent that no two species which have overlapping distributions have the same physiological responses and therefore probably do not occupy the same "niche." Thus competition between these desert species is minimized, a distinct advantage in an area where resources of food and water may fluctuate either seasonally or yearly.

The role of natural selection in fitting a particular species for the desert environment is difficult to assess because of the complex relationship between the phylogenetic background of the species, the "niche" occupied by a species, and the rate at which evolution can occur in response to a changing environment. However, it can be pointed out that natural selections need only act in the direction of effectiveness of solution for a particular "niche" and need not be concerned with elegance of mechanism.

While diverse behavioral and physiological adaptations for coping with the desert environment have already been found among birds and mammals living and reproducing in this region, many

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species occupying special niches remain to be studied. Recently we have examined the physiological performances of the Poor-will (Phalaenoptilus nuttallii) and three species of ground squirrels (Citellus mohavensis, Citellus tereticaudus, and Citellus leucurus). Our results illustrate some additional types of adaptations to the desert environment. The ground squirrels are fossorial and diurnal; hence, they occupy an ecologically intermediate position between the small nocturnal and large diurnal mammals. The Poor-will is crepuscular, although it may nest and roost in areas of extremely high temperatures.

The Poor-will has a basal metabolic rate one-third of that predicted from the equation: $\text{ccO}_2/\text{gm}/\text{hr} = 9.3 W^{-0.36}$. Because of its low standard metabolic rate, the lower critical temperature of the Poor-will is also very high (Fig. 1). This low metabolism minimizes the amount of metabolic heat to be dissipated, a useful adaptation when a small difference between body and ambient temperatures precludes much radiation, convection, and conduction of metabolic heat.

In order to prevent the elevation of body temperatures to lethal levels when high ambient temperatures are encountered, many birds and some mammals pant. The metabolic heat production associated with panting increases the evaporative water loss and is expensive to the water economy, a major consideration for animals of arid regions. However, unlike many birds, the Poor-will does not pant and therefore has no marked upper critical temperature. Although the thermal neutral zone begins at a rather high lower critical temperature, it is also very broad (Fig. 1) and extends at least to 44°C . At ambient temperatures above 40°C , the extensively vascularized gular area is fluttered rapidly with the mouth held open. In this way, the bird is able to dissipate its metabolic heat (in addition to dissipating heat gained from the environment when the ambient temperature exceeds the body temperature) while simultaneously keeping its level of heat production virtually unchanged. At high ambient temperatures, the amount of water expended by the Poor-will for evaporative cooling is less than that expended by other birds of comparable size (Fig. 2). The combination of a low basal metabolism and a gular flutter which does not increase the metabolic rate necessitates only a modest level of evaporative water loss in

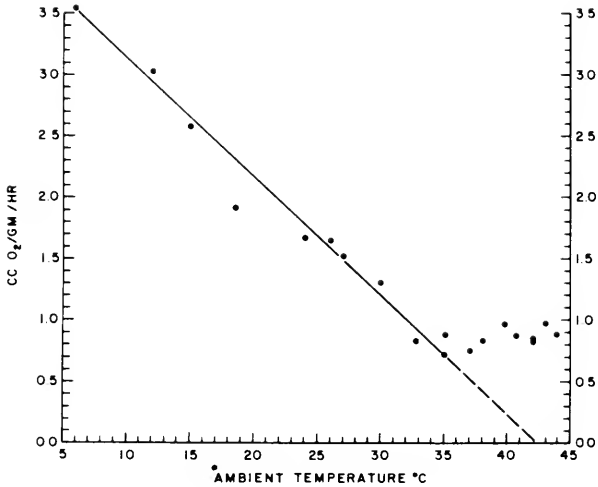


Figure 1. Oxygen consumption (corrected to STP) of a Poor-will (*Phalaenoptilus nuttallii*) plotted against ambient temperature. Each point is the minimum consumption maintained for at least 30 minutes in a post-absorptive bird. The solid line is fitted by eye and is extrapolated as the dashed line to intercept with the abscissa. This intercept indicates only an approximate conformity with Newton's Law of Cooling.

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SPECIES	WT (GMS)	MGMS H ₂ O/GM/HR	REFERENCE
		T_A (°C) = 32-33°	37-38°
			42°
<u>Richmondia cardinalis</u>	38-48	3.7	8.0
			20.0
<u>Pipilo aberti dumeticolus</u>	47	7.0	13.0
			25.0
<u>Phalaenoptilus nuttallii</u>	40	4.8	3.0
			9.0
			This study

Figure 2. Evaporative water loss in three species of birds at selected ambient temperatures. The data were estimated from the graphs of Dawson (1954, 1958).

order for this species to dissipate all of its metabolic heat and heat gained from the environment when the T_A exceeds the T_B (Fig. 3). Since at high ambient temperatures, other species of birds comparable in size with the Poor-will become hyperthermic and elevate their metabolism when panting (Dawson, 1954; Dawson and Tordoff, 1959), it is difficult to use comparisons for evaluating the reduction in evaporative water loss accruing from the Poor-will's reduced metabolism. However, it may be noted that if there is no radiation-convection-conduction of metabolic heat, as would occur in the Poor-will when the body and ambient temperatures are equal (40°C), a 40 gram bird with a metabolism one-third of normal saves 12 cc of water/day (assuming that one cc of oxygen releases 4.8 calories and 1 mgm of evaporated water dissipates 0.58 calories).

Scholander (1955) has suggested that evolutionary adaptation for temperature regulation in homeotherms has principally involved heat dissipation and that heat production has not been modified since all species, regardless of habitat, typically follow the mouse to elephant curve. Thus, arctic mammals at low ambient temperatures keep their heat dissipation minimal by virtue of good insulation and possess special means for dissipating heat during activity or at relatively high ambient temperatures. In contrast to arctic mammals and birds, animals from desert areas more frequently encounter problems of maximizing heat dissipation when there is a small difference between body and ambient temperatures. For this reason, it might be expected that at least some species, particularly those which are diurnal, would demonstrate a reduction in the level of basal metabolic heat production. The Poor-will is an example of such a species, and thus it is an exception to Scholander's generalization that metabolism is not adapted to climate. Although Scholander et al. (1950) relate the low metabolism of tropical caprimulgids to their capacity to hibernate, such a correlation does not differentiate between cause and effect. Thus, hibernation may either allow or follow a low basal metabolism. Also, considerable evidence has accumulated to suggest that the low metabolic rate of many hibernators may be attributable to the fat deposits which in themselves probably exert little effect on the overall metabolism (Bartholomew and Hudson, 1960; unpublished observations on Citellus tereticaudus and Cercaertus nana). Therefore, it is probably neces-

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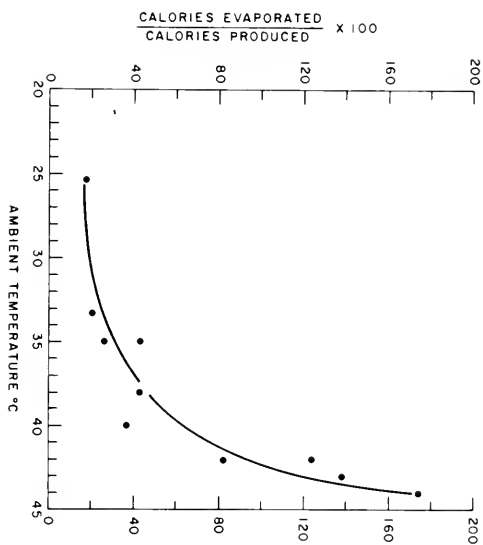


Figure 3. The relation of evaporative cooling to metabolic heat production in the Poor-will exposed to various ambient temperatures. The calculations assume that the consumption of one cc of O_2 yields 4.8 calories and that the evaporation of one mg of water requires 0.58 calories.

sary to use fat-free weights for comparing the basal metabolic rates of hibernators and non-hibernators, in order to be certain that a low metabolic rate is a phenomenon typical of hibernators.

The high lower critical temperature (35°C) in the Poor-will means that much of the time this species lives outside its thermal neutral zone. It is interesting to note that the Poor-will undergoes seasonal torpidity when food is less available and when the maintenance of a normal body temperature would be metabolically expensive (Bartholomew, Howell, and Cade, 1957). While there are other species of birds which spend much of their time outside the thermal neutral zone (Dawson and Tordoff, 1959; Scholander et al., 1950), torpor is particularly advantageous in the Poor-will, because this species represents an unusual combination of specialized morphological and behavioral adaptations for foodgetting, with its food sources subject to marked fluctuation in availability.

The low basal metabolic rate of the Poor-will is reflected in a low heart rate (Fig. 4) at thermal neutrality. Birds which are comparable in size to the Poor-will but which possess a normal metabolism (Odum, 1945) have heart rates about twice that of the Poor-will. While both heart rate and metabolism increase when the ambient temperature decreases below the lower critical temperature, the heart rate reaches its maximum level at a T_A of about 15°C , whereas the metabolism continues to increase as the T_A decreases below 15°C .

Seasonal torpidity as a thermoregulatory adaptation for low temperature is a well documented phenomenon among mammals. Although numerous natural history accounts have suggested that seasonal torpidity may also be a response to conditions of high temperatures and limited availability of food and moisture, there are only a few studies of the physiological performance of animals which utilize summer torpor or aestivation (Bartholomew and Cade, 1957; Bartholomew and Hudson, 1960; Bartholomew and MacMillen, 1961).

The ecological stimulus for aestivation is difficult to identify precisely in all of the species known to aestivate because of the

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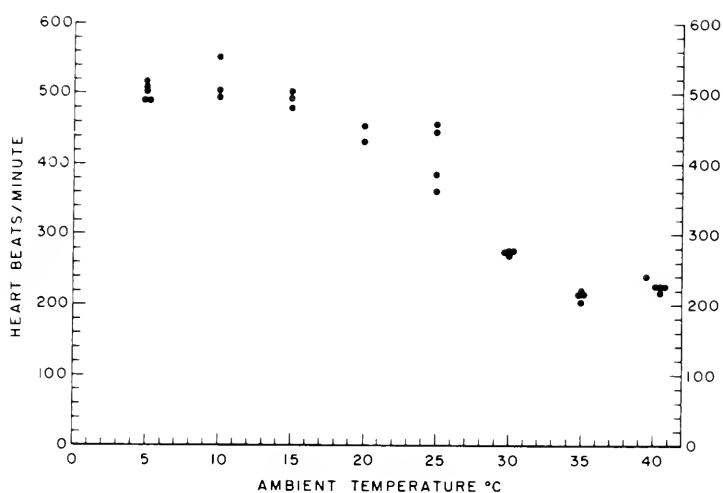


Figure 4. Heart rate of a Poor-will at different ambient temperatures. The closed circles represent the heart rate of an inactive bird following at least 30 minutes of exposure to each ambient temperature.

complex interrelationship between availability of food and water and the prevailing temperature. However, some of the pocket mice, which can maintain themselves on a dry diet (Perognathus longimembris, P. xanthonotus, P. formosus, P. penicillatus and P. fallax) become torpid when food is withheld (Bartholomew and Cade, 1957); furthermore, P. californicus has a daily cycle of torpidity which is related to the degree of deprivation of food (Tucker, 1961).

Adaptation of two species of ground squirrels, C. mohavensis and C. tereticaudus, to the desert environment depends in part on their capacity to become torpid. The mohave ground squirrel (Citellus mohavensis) readily becomes torpid at laboratory temperatures throughout the year, despite the continuous availability of food. Episodes of torpor are less frequent from March to August, which is their period of activity under natural conditions. When entering torpor at ambient temperatures between 22°C and 26°C , they assume the usual sleeping posture, their oxygen consumption declines rapidly, and body temperature approximates environmental temperature within 3 or 4 hours. During torpor, oxygen consumption is less than 0.2 cc/gm/hr, and the animal breathes irregularly, with marked periods of apnea. Following the onset of arousal, oxygen consumption increases 10- to 20-fold, and it usually peaks within 20 minutes. Body temperature increases more slowly, and the levels of body temperature characteristic of normal activity are usually attained in 45 to 60 minutes. Typically, rectal and oral temperatures are within 0.5°C of each other during arousal. This pattern for the onset of torpor, torpor itself, and arousal from torpor in the mohave ground squirrel is typical of the classical picture of hibernation and occurs at ambient temperatures between 10°C and 27°C (the highest measured). Under natural conditions, this species is torpid during part of the hot, dry periods and continues this pattern throughout the winter at a time when food and water are relatively scarce. Thus, the physiological mechanisms for torpidity appear to be the same during both summer and winter, although the level of body temperature may differ.

In contrast to Citellus mohavensis, C. tereticaudus kept in the laboratory throughout the year with food and water available demonstrated intermittent periods of torpidity from June to October only. Animals with body temperatures within a degree of room tempera-

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ture demonstrated the typical arousal pattern when disturbed (Fig. 5). The difference between oral and rectal temperatures during arousal was never more than 3° C, and arousal was accompanied by strong visible shivering. Animals attained a normal body temperature within 45 to 60 minutes after the onset of arousal at room temperatures. No instance of torpor was observed between November and May in a captive round-tailed ground squirrel. Furthermore, between November and May, the body temperatures of animals were much less variable and averaged higher than those found between June and October (Fig. 6). It appears from the laboratory performance of C. tereticaudus that this species may aestivate, but not hibernate. This suggestion is supported by collection records (Donald R. Dickey collection), which indicate that this species has been trapped in December, January, and February in the Coachella Valley, California. Since C. tereticaudus has been readily trapped during the summer and early fall, aestivation under natural conditions must occur on either a daily or an intermittent basis.

It is striking that aestivation is characteristic of one member of a sympatric pair of desert ground squirrels. The ranges of C. tereticaudus and C. mohavensis are overlapped by C. leucurus, but C. tereticaudus and C. mohavensis do not occur in the same area. C. leucurus neither aestivates nor hibernates, but remains active above ground at all times of the year. Thus, in the area of sympatry for these desert ground squirrels, only C. leucurus is active during the more demanding and difficult parts of the year. It seems reasonable, therefore, to postulate that between these sympatric ground squirrels competition, in the sense of utilization of a common resource which is in short supply (Birch, 1957, p. 6), perhaps is reduced, except in very poor years, because of the differences in the seasonal patterns of their metabolism.

In contrast to the diurnal ground squirrels which aestivate or to the nocturnal rodents which are fossorial, C. leucurus must cope with much of the rigor of the desert environment throughout the year. The antelope ground squirrel depends on some of the types of physiological mechanisms similar to those utilized by the Poor-will, the kangaroo rat, and the camel in adapting to desert conditions (Hudson, 1962). Like the Poor-will, the antelope ground squirrel has a broad thermal neutral zone with a relatively high lower critical

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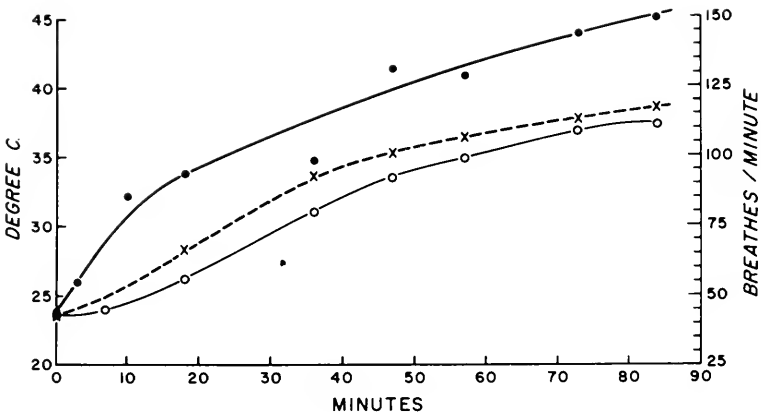


Figure 5. Body temperature and respiratory rate of a round-tailed ground squirrel (*Citellus tereticaudus*) during an arousal at room temperature (22° C to 25° C). The bottom line is the rectal body temperature; the middle line is the oral body temperature; and the top line is the respiratory rate.

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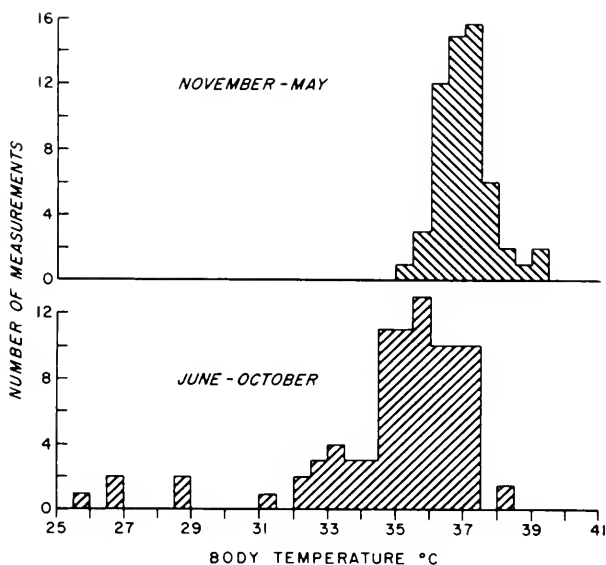


Figure 6. Body temperatures of 12 *Citellus tereticaudus* measured periodically during the year. Individual measurements were grouped into 0.5 degree intervals. The heights of the histogram represent the frequency at each interval. The separation of June to October and November to May measurements were based on the occurrence of spontaneous torpor at room temperature in the first category and its absence in the second category.

temperature and no marked upper critical temperature (Fig. 7). Unlike the Poor-will, the antelope ground squirrel has a basal metabolic rate conforming to the predicted value $cc\ O_2/gm/hr = 3.8\ W^{-0.27}$). C. leucurus can tolerate ambient temperatures of $42.6^\circ\ C$ for periods of at least 2 hours, whereas many of the nocturnal rodents of similar size cannot withstand ambient temperatures above $40^\circ\ C$ for equivalent periods of time (Dawson, 1955; Lee, 1960; unpublished observations, Carpenter, 1961; and Tucker, 1961). The body temperature of C. leucurus increases linearly with ambient temperature when the ambient temperature increases from room temperature to $40^\circ\ C$ (Fig. 8). Thus, the antelope ground squirrel depends on hyperthermia both to minimize heat gain from the environment at high ambient temperatures and to maximize loss of metabolic heat by radiation, convection, and conduction. When the difference between T_A and T_B is inadequate for dissipation of metabolic heat by radiation-convection-conduction and pulmonary evaporation of water (Fig. 9), C. leucurus drools copious amounts of saliva, which it actively spreads over parts of the body.

Under natural conditions, C. leucurus probably avoids prolonged exposures to very high ambient temperatures, which would be expensive to the water economy, by periodically returning to the cooler burrow. An animal requires only 3 minutes to reduce its body temperature from $42^\circ\ C$ to $38^\circ\ C$ when taken from a T_A of $42^\circ\ C$ to $25^\circ\ C$. In this way, a hyperthermic animal can unload accumulated heat within the burrow and then return above ground. From this, it is apparent that behavior can be an important factor in relating the thermoregulatory capacity of this species to the prevailing environmental temperatures.

Any consideration of the problem of thermoregulation at the high ambient temperatures of the desert must take into account the availability of water and the capacity of a species to conserve water. The ability of the antelope ground squirrel to maintain a positive water balance under desert conditions is a complex inter-relationship between several factors: its type of food, its level of pulmocutaneous water loss, and its capacity to conserve water incidental to excretion and defecation. While each of the above factors may be studied separately under laboratory conditions, their synthesis in relation to natural conditions is extremely dif-

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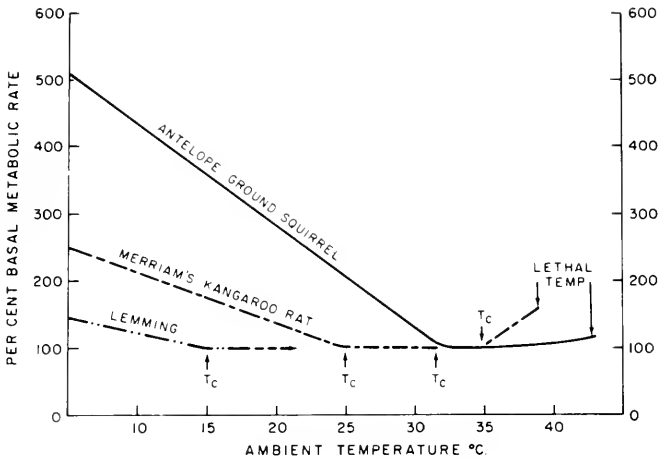


Figure 7. Metabolic rate at different ambient temperatures expressed as percentage of basal values for three species of rodents: the arctic lemming (Scholander et al., 1950), the nocturnal kangaroo rat (*Dipodomys merriami*) (unpublished observations, Carpenter, 1961), and the diurnal ground squirrel (*Citellus leucurus*) (Hudson, 1960).

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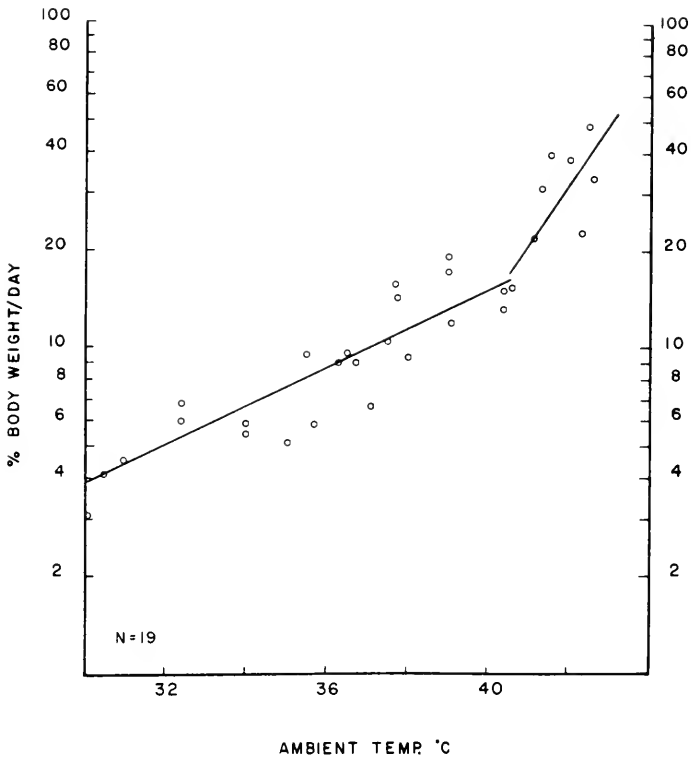


Figure 8. Evaporative water loss in 19 *Citellus leucurus* at different ambient temperatures. The line between 30° C and 40° C is described by the equation $Y = (0.0431)(1.159)^X$. The break in the two lines denotes the onset of copious salivation.

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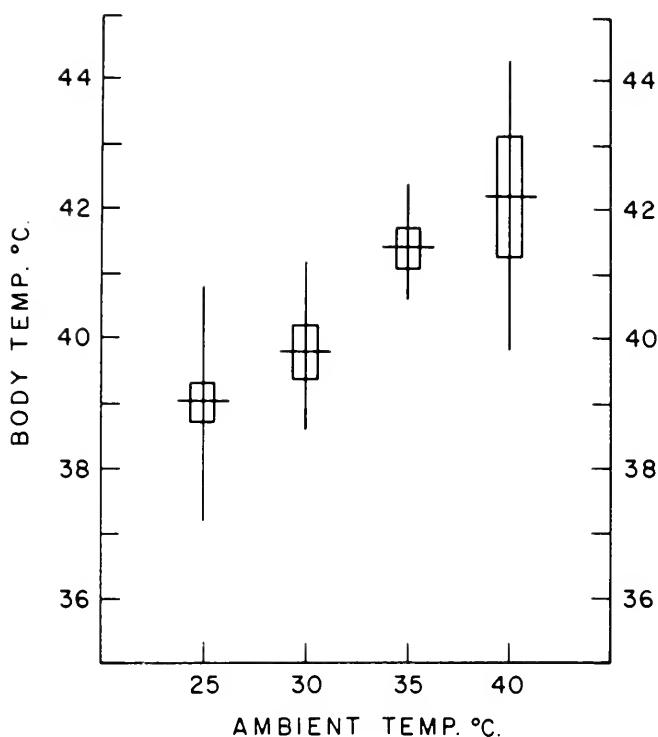


Figure 9. Body temperatures of normally active *Citellus leucurus*. The vertical lines indicate the range; the horizontal lines indicate the mean (M); the rectangles indicate the interval $M + 2 s_m$ to $M - 2 s_m$. The temperature below each vertical line is the ambient temperature.

ficult. However, it is possible to compare the abilities of C. leucurus and other desert rodents to minimize excretory water loss. Such a comparison serves as a basis for acquiring insight into their relative dependence on water ingestion.

The capacity of some of the heteromyids to keep urinary water loss at a minimum by the production of a very concentrated urine is well known. However, there is little information on other desert species. Direct comparison of renal concentrating capacity among species which may differ slightly in kidney performance is complicated by the variability of kidney function; this is in part related to variations in ambient temperature, diet, and fluid intake. For example, animals given water ad libitum show a correlation between the urine concentration and ambient temperatures (Fig. 10). Furthermore, because of the possibility of active transport of urea in the renal tubules (B. Schmidt-Nielsen, 1960), a high protein diet may increase solute excretion without causing an appreciable increase in excretory water loss. Single measurements of urine concentration in animals deprived of water tells little of the minimum daily water loss required for the discharge of excretory wastes.

One useful technique for comparing different species is to measure the concentration of urine produced over a 24 hour period (with comparable diets) when a species is drinking only enough water to maintain body weight. Data on average urine concentration per 24 hours while drinking a quantity of water minimal for weight maintenance are presented for C. tereticaudus (Fig. 11).

In order to compare the renal concentrating capacity of C. tereticaudus with other species, it is necessary to assume that the serum has a solute concentration of approximately 350 milliosmols and then to divide the urine concentration by this figure. On the basis of this assumption, the daily urine concentration of C. tereticaudus averages eight times the serum concentration. The average ratio of urine and serum concentrations in the kangaroo rat (D. merriami) as estimated from the data of Schmidt-Nielsen et al. (1948a, 1948b) is 10.3 when the animals are on a normal diet and 12.1 when animals are eating soybeans. The antelope ground squirrel has a urine-serum ratio of 9.7 when deprived of water (Fig. 12). Although values from all of the species are difficult to compare, it

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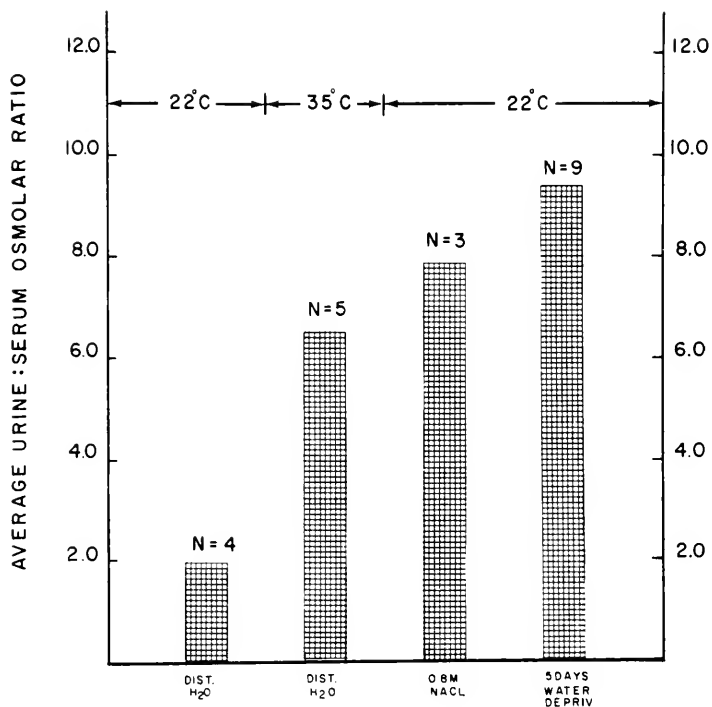


Figure 10. Ratio of urine and serum osmolar concentrations for *Citellus leucurus* subjected to the various conditions of water availability described below each rectangle. Arrows denote the ambient temperature to which animals were exposed. N indicates the number of animals.

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Regimen	Milliosmols		N	Urine Volume (cc)		Body Weight	
	Mean	Range		Mean	Range	Mean	Range
Drinking distilled water <u>ad libitum</u> ; single samples	975	260-2800	25	---	---	194.1	132.8-251.0
Drinking minimum water; urine collected overnight	2350	1949-2802	9	1.2	0.6-1.8	176.1	142.2-225.0
Drinking minimum water; urine collected during the day; single samples	3453	2377-4012	11	---	---	176.3	111.0-233.0
Deprived of water; urine collected overnight	3093	2690-3550	6	.4	0.1-0.7	160.9	127.0-202.8
Deprived of water; urine collected during the day	2792	2324-3254	5	.2	0.1-0.3	160.9	127.0-202.8

Figure 11. Volume and concentration of urine collected from 11 *Citellus tereticaudus* maintained at room temperature. Urine was either allowed to accumulate under oil for a period of time prior to measuring its concentration, or it was measured immediately after voiding (single samples).

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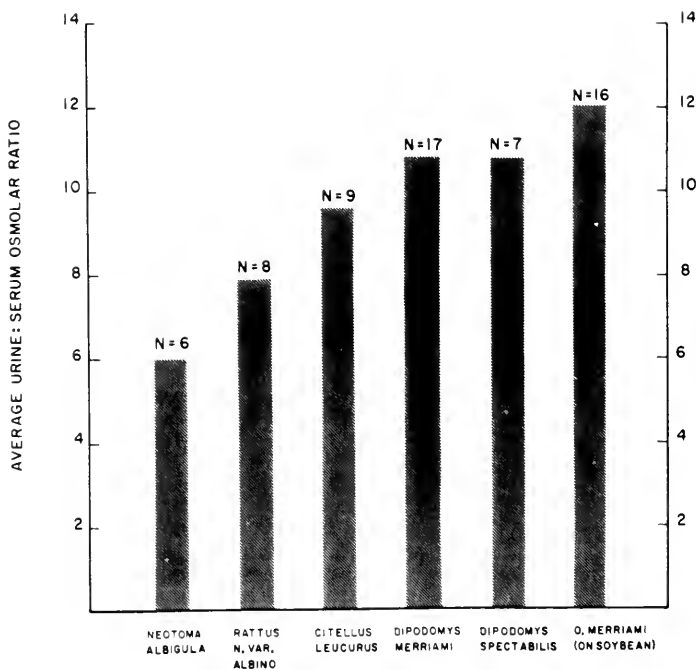


Figure 12. Renal concentrating capacity of various rodents maintained on a dry diet. The urine:serum osmolar ratios of species other than *C. leucurus* are estimated from the data of Schmidt-Nielsen et al. (1948a, 1948b).

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appears that the ground squirrels produce a urine less concentrated than that of the kangaroo rat (D. merriami), but more concentrated than the urine of the wood rat (N. albigula). Also, the antelope ground squirrel (C. leucurus) produces a urine more concentrated than that of the round-tailed ground squirrel.

Significantly, the kangaroo rat, which is the species producing the most concentrated urine, is primarily a seed eater, and can maintain body weight on a dry diet. It is suggested that under natural conditions the daily water requirements of the diurnal ground squirrels are too large to allow dependence on the water content of a typical seed diet even if the kidney were better able to concentrate urine. Thus, while ground squirrels cannot maintain themselves on a dry diet, they have a renal concentrating capacity sufficient to balance the routine water losses with the water available in their diet of succulent foods.

SUMMARY

Birds and mammals living in the deserts utilize a variety of physiological, morphological, and behavioral patterns which may be subjectively judged as varying from "well adapted" to "poorly adapted." In all cases, the ability of a desert species to live and reproduce in its environment indicates adaptation regardless of the elegance of the mechanisms utilized. The role of natural selection is such that effectiveness of solution rather than any special mechanism is the primary criterion.

The multiplicity of adaptive mechanisms attests to the diversity of niches available, and it may turn out that no two desert species of similar distribution have identical morphological, physiological, and behavioral adaptations. While there are many species which remain to be studied, data for the Poor-will (Phalaenoptilus nuttallii) and three species of ground squirrels (Citellus leucurus, Citellus tereticaudus, and Citellus mohavensis) further demonstrate the diversity of adaptive mechanisms.

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The Poor-will has a basal metabolism which is one-third the predicted value and is thus an exception to Scholander's generalization that metabolism is not adapted to climate. The combination of a low basal metabolism and a gular flutter which does not significantly increase metabolic heat production enables the Poor-will to dissipate all its metabolic heat at high ambient temperatures, with a minimum expenditure of water. At thermal neutrality, the low basal metabolism of the Poor-will is accompanied by a heart rate which is one-half the value found in birds of comparable size. Because of a low basal metabolism, the Poor-will also has a high lower critical temperature and may therefore spend much of its time outside the thermal neutral zone. It is significant that this species hibernates during the winter when it would require a great deal of food for maintenance of a normal body temperature.

While the stimulus for the onset of torpidity in those species of desert mammals known to aestivate is not clearly defined, limitation of food in at least two species, Perognathus longimembris and Perognathus californicus, causes periodic torpor.

Hibernation and aestivation in the mohave ground squirrel illustrate the same physiological characteristics and are differentiated only by the level of body temperature during torpor and the season in which torpidity occurs.

Under laboratory conditions, the round-tailed ground squirrel (C. tereticaudus) is intermittently torpid during the summer and fall, but does not become torpid during the winter or spring. Therefore, in terms of natural history, this species could be considered to be an aestivator and not a hibernator.

It is postulated that competition, in the sense of utilization of a common resource which is in short supply, between the sympatric desert ground squirrels is minimal because of differences in their patterns of metabolism.

The antelope ground squirrel, which is not capable of torpidity has a broad array of thermoregulatory mechanisms adaptive for its

niche. Among its adaptive patterns are: (1) tolerance of ambient temperatures up to 42.6°C for periods of 2 hours, (2) a thermal neutral zone extending from 30°C to 42.6°C without a marked upper critical temperature, (3) supplementary evaporative cooling by active spreading of a copious secretion of saliva over the body when the ambient temperature exceeds 39°C , (4) dependence on hyperthermia even at low ambient temperatures (30°C) for radiative-convective-conductive dissipation of heat, and (5) effective capacity for unloading accumulated body heat, by periodically returning to the cooler subterranean environment.

In an ecological context, problems of thermoregulation for desert birds and mammals become intimately linked to the complex interrelationship between availability of moisture, level of pulmonary water loss, and capacity for water conservation. A comparison of renal concentrating capacity among several desert rodents offers some insight into the extent of adaptation for water conservation. Ranking those species for which data are available in order of ability to concentrate urine one obtains the list: D. merriami > Citellus leucurus > C. tereticaudus > Neotoma albigula. Only D. merriami, which is primarily granivorous, is able to maintain body weight on a dry diet while the ground squirrels and wood rats depend on availability of succulent foods to satisfy their water requirements.

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HUDSON

DISCUSSION

VEGHTE: What is your definition of torpor; and is it reproducible?

HUDSON: Do you mean is torpor reproducible in the particular species? Can I get an animal repeatedly in torpor? Yes, it is very reproducible. We define torpor in two ways. First of all, the animal has a body temperature which is within a degree or so of the environmental temperature, and then secondly, he must be capable of spontaneously arousing so that we could not include any application of heat in order to get arousal for the animals. Incidentally this spontaneous arousal is accompanied by shivering and other classical manifestations of hibernation.

HANNON: While you are defining things, would you define "estivation"? Is there any difference between the two?

HUDSON: Well, it looks like there is not, at this point. I think a lot more work has to be done. I am not absolutely convinced that there are not some subtle differences in the physiological mechanisms of estivation and hibernation so that, as of now, estivation is the hibernation response which occurs in the summer, and, therefore, occurs at fairly high ambient temperatures.

HANNON: I am asking about torpor versus estivation. Is it the same or different?

HUDSON: Well, it seems to me this kind of thing right now is only a matter of opinion about usage of the word "torpor" rather than being based on very much factual information. I am of the opinion that estivation is a much more intermittent and brief kind of a response than hibernation. Certainly both cases illustrate torpor.

WEST: I would like to comment on the difference between results on heart rate responses of desert birds compared with the sub-arctic birds that we have been working on. We find that there is a continual linear relationship of heart rate to decreasing

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temperature as far down as we record it, and this goes to a little below 0° C. We found we cannot get any leveling off as high as we have measured it, which is about 32° C. You do not find a leveling off or thermo-neutral zone type of thing, as Dr. Hudson found in the Poor-will. We found also that at the very low temperature, the shivering was so intense that it obscured the heart rate except at very short intervals, when the heart rate would come through. I wondered how you recorded your heart rate.

HUDSON: Of course, we started off by measuring it in the thermal neutral zone and the Poor-will is probably a particularly good bird for this sort of thing, since it is quite tractable. As we get below the lower critical temperature of course the shivering begins to appear on the EKG record, but does not make it impossible to pick out the QRS complex until we begin to get down to ambient temperatures around 20° C. Now, at those temperatures, we have found that by giving the bird, and it appears to have an extremely rapid and sensitive response to this, a quick burst of heat, not enough to seriously interfere with its metabolism or its body temperature in any way, that it will immediately cut out shivering and then we can pick up a clearer EKG record. Then in a matter of minutes, of course, it starts to shiver again. I would like to counter by asking you a question, and that is: do you find any sort of a correspondence between the lower critical temperature of the heart rate and metabolism, or are all your measurements of heart rate made in the thermo-neutral zone?

WEST: I never find a thermo-neutral zone for the small birds I have studied. I never go to high enough temperatures. Unfortunately, we are so concerned with cold, we do not go much over 30° C.

HUDSON: Most of the small birds have a thermo-neutral zone or point that would be around or above 30° C.

WEST: But we get perfect linear correlation of temperature on metabolism and on heart rate, as far as we can go up and down.

HUDSON

HUDSON: This is the kind of thing that will just take more measurements of different kinds of birds.

WEST: I am interested in seeing the way your heart rate falls off at the lower temperature, then goes flat; yet the metabolism continues to fall.

HUDSON: This may be a factor that is associated with hibernation, because these are all species of birds and mammals which have the capacity to hibernate or estivate.

WEST: There must be a change in the stroke volume.

HUDSON: Yes, if I can assume you mean that it is suggestive that the stroke volume changes at the place where the heart rate levels off?

WEST: Yes.

HART: Or the utilization.

HUDSON: Yes, utilization or both.

VEGHTE: What is the duration of the burst of heat?

HUDSON: No more than a couple of minutes.

WEST: I think this is probably a safe technique; we are trying to measure heart rates in flight. We let the birds fly for a few wing beats and as soon as they hit the ground, we get the heart rate, which is extremely fast. We get it the instant that they stop flying. I know there is a small lag there but I think that this same heart rate does carry through.

HUDSON: We have also been able to pick out rates that correspond with the ones that we get where we have given them bursts of heat from records that have very intense shivering on them.

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WEST: I think that with the technique I mentioned yesterday, the power frequency distribution, we can single out the heart rate. It is so constant. It comes out as a peak in the power spectrum, no matter how much shivering is masking it on the oscillograph record.

IRVING: Do you give a Poor-will any test to find what its mental state is in a thermo-neutral zone? Is it entirely alert? Can it still do multiplication?

HUDSON: Well, he recognizes me in the thermo-neutral zone. I do not know whether that is a very good test or not.

IRVING: You do not see any noticeable signs of a mental state characterizing torpidity? That would be my main question; is that a normal resting basal rate?

HANNON: I noticed in your oxygen consumption of the Mohave ground squirrel, going in and out of torpor, that he lowered his oxygen consumption as he went into torpor. It looked like he may have lowered it more than he should. When he came out it appeared that there was an oxygen deficit. The oxygen consumption went way up.

HUDSON: This is overshoot. Yes, this is characteristic in arousing from hibernation, and I am not entirely clear on what this may all mean in terms of the internal physiology of the animal, at that time, whether there is some sort of a heat storing going on, assuming that the overshoot does not coincide with attainment of a normal body temperature. It is easier to explain in animals that restrict the development of body temperature to the fore quarters which is different from our desert ground squirrels. That is, for instance, the 13 lined ground squirrel on arousing from hibernation, typically has the anterior end of the animal developing normal body temperature first before the posterior end does, and we get no such responses. That is, we have never observed anything like this and we assume that it is related to the fact that these animals have rather high body temperatures to begin with.

HUDSON

EAGAN: Do these animals shiver as they are coming out of torpor?

HUDSON: Yes. The magnitude of the shivering tends to vary from one individual to the next, but there seems to be no difference in rate of arousal correlated with this. One gets almost the impression that there is some inefficient use of shivering going on in some individuals.

EAGAN: I think this could explain the higher metabolism. Because after all, when the animal is completely back to body temperature, then it does cease its shivering.

HUDSON: This would be the explanation for the actual heat production itself.

EAGAN: And the overshoot?

HUDSON: Yes. Shivering of course will continue on beyond the overshoot.

JOHANSEN: Have you tried to look for any vascular changes in the legs by measuring superficial temperatures?

HUDSON: No, we have not.

HANNON: Has there been any measurement of changes in blood chemistry during the course of torpor? I am getting back to this increase in oxygen consumption, and particularly, I would think of lactic acid. Is there an accumulation of lactic acid?

HUDSON: I do not know. The intubation technique that Lyman has extended promises to be a good means for finding this kind of information.*

*Lyman, Charles P. and Regina C. O'Brien. 1960. Circulatory changes in the thirteen-lined ground squirrel during the hibernating cycle. Bull. Mus. Comp. Zool. 124:353-372.

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EAGAN: I was surprised at the rapid and dramatic drop in body temperature in the species you mentioned. Was that the antelope ground squirrel?

HUDSON: When he was overheated?

EAGAN: Yes.

HUDSON: This is the antelope ground squirrel.

EAGAN: And how many minutes was that, did you say?

HUDSON: Three minutes. Of course this is a small animal.

EAGAN: Is this accomplished just through transfer through cooler air, or is it through conduction in the burrow walls?

HUDSON: Well, he was transferred into an environment where the temperature was all the same, so this is artificial, but the substrate temperature was the same as the air temperature, so conduction would be an important factor here. They show an interesting behavioral response to this; when they become overheated or become relatively warm and have the opportunity to spread out on a cooler surface, they do this by extending their legs out, lying very flat, and very close to the surface; this has also been reported by people living in the desert where they can observe these animals coming into the shaded areas or on to moist concrete.

MORRISON: If you put the animal back at 42° C, how long does it take him to rewarm? In other words, if it took three minutes to cool, how long will the reverse process take?

HUDSON: We have not done that.

HART: Have you calculated the basal metabolic rate of the Poor-will in absolute units at the thermo-neutral zone?

HUDSON: In terms of calories?

HUDSON

HART: Yes.

HUDSON: No, I just did it on the basis of oxygen consumption.

HART: You made the point that it was very low. I was wondering if this was in relation to body size.

HUDSON: This is in relationship to body size. It is using the equation from Brody in assuming that one cc of oxygen consumed releases 4.8 Calories.

PROSSER: Does this metabolism fall below the standard curve?

HUDSON: Yes. It falls about 66% below the standard curve.

IRVING: What does torpor mean in the dictionary? Does it not mean a decline in brightness? I am still interested in the napping state. I was thinking there might be some other observation that you could make other than whether the Poor-will recognized you or not at the thermo-neutral zone.

WEST: Any way to test his reaction?

IRVING: To show whether he was alert or not, or whether he was taking a nap.

HUDSON: Well, they will feed. I know that the animal is not in a torpid state at what we call thermo-neutrality because he will feed quite regularly. Now, if you force feed him when he is torpid, he will die, apparently because of the decomposition of food in the gut under those situations, and yet when they are not torpid they can be fed successfully. Of course a torpid animal will have his eyes closed.

IRVING: But in the thermo-neutral state, they feed and eye reflexes are apparent, seem to be perfectly normal?

HUDSON: Yes, perfectly normal.

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IRVING: I think that is very rare with the metabolism diminished to one-third of the normal. But every means possible should be taken to be sure we are dealing with a more or less regular animal.

HUDSON: Well, they can fly.

IRVING: Can they take off instantly?

HUDSON: Oh, yes, if you open the cage a little too laxly, why they are gone.

KLEIBER: What saves these torpid animals from predators? Is there something which protects them?

HUDSON: As you may or may not know, a lot of the success of this laboratory in working with Poor-wills is because of human predators who have found torpid Poor-wills on their front lawn and back yard and in the library. This is the way in which we have acquired most of our Poor-wills, and I assume that predation must be rather severe.

IRVING: Maybe they do not taste good.

HUDSON: You do not know that until after you have eaten them.

