GENERAL SURVEY OF THERMOREGULATION IN BIRDS AND MAMMALS.
Temperature, the limiting factor of chemical reactions, determines growth and metabolism of the living organism. Perhaps more than other environmental factors, temperature has multiple and diverse effects on living organism, it limits the distribution and survival of animals on the earth.

Poikilothermic or cold-blooded animals, the greater part of the animal kingdom, which have a temperature slightly below that of the environment, respond to changes in environmental temperature by conforming passively to the environment. Comparatively few animals can regulate their body temperature; these are the mammals and birds which maintain a temperature above that of their normal environment, and are known as the warm-blooded or homoiothermic animals. The animals which have limited temperature regulation are known as heterothermic animals. Warm-blooded animals can react to extreme environmental temperature by protective behaviour and for this reason is aptly described as a "homoiotherm" — capable of maintaining constancy of temperature — in contrast to the "poikilotherm", an animal whose temperature varies passively with that of the environment.

In the poikilothermic animals the factors producing body heat tend to equal the factors favouring loss of heat, and the body temperature approaches environmental temperature. The temperature relations of poikilothermic animals are different according to whether they live in dry or moist air or in water. The evaporative heat loss is greater in dry air than in moist air and in water the heat loss is by conduction and convection. In amphibia the temperature relations are closely related to their water balance (Adolf, 1932, 1942; Kirk and Hogben, 1946; Mellanby, 1941). Frogs lose water in proportion to their relative humidity, but are unable to absorb water—even from air saturated with moisture because their
metabolic heat results in some evaporation. It is reported by Benedict (1932) that the metabolism of an amphibian calculated for 37°C is only one-fifth that of a mammal (mouse) of comparable size. According to Morgan (1922) the skin of frog contains receptors, which are clearly distinct from touch, pressure and pain receptors, for both heat and cold and the spinal reflexes are elicited when the heat receptors are stimulated at 39 to 43°C and cold receptors at 10°C.

The largest poikilotherms are the reptiles from whom the homoiothermic animals arose. Reptiles are less concerned with humidity and their body fails to cool significantly when the humidity decreases at a constant air temperature (Hall and Root, 1930).

Poikilotherms lack efficient mechanism of heat retention. Their metabolic activity is limited in low environmental temperature and in higher temperature distribution of heat from the body surface depends largely on an active circulatory system. Rodbard (1947, 1948) and Rodbard and Feldman (1948) demonstrated that in turtles and frogs there is a direct relationship of arterial blood pressure with blood temperature and the blood pressure is no longer responsive to temperature when the brain is pithed. It has also been demonstrated that local warming or cooling in the hypothalamus of the turtle but not other regions of the brain has an effect on blood pressure. The diastolic pressure of unanaesthetized mammals including dog (Katz et al, 1939; Rodbard and Katz, 1945), rabbit (Rodbard, 1940), man and rat is about 80 mm Hg and these mammals have body temperature approximately 38°C, while the chicken (Rodbard and Tolphin, 1947), turkey and duck (Rodbard, 1948) have diastolic pressures of 120-140 mm Hg and correspondingly higher body temperature.
Homoiotherms, the mammals and birds, are the highest forms of life. The maintenance of constancy of internal environment is of fundamental importance to the life of the organism and the temperature of this environment, namely that of the circulating blood, is considered to be just as important as its chemical composition and pH. Birds and mammals have a temperature sensitive centre in the brain and in this respect they differ from all other animals. This temperature sensitive center acts as a thermostat of the body by heat production and heat retention. Cooling and warming mechanisms come into more prominent action in high or low environmental temperature respectively so that the body temperature is relatively constant over a limited external temperature range. However, the body temperature shows diurnal fluctuations associated particularly with muscular activity, feeding and digestion. In large birds the diurnal temperature variation is less than in small birds, the nocturnal birds, such as the owl have their temperature maximum during the night (Simpson and Galbraith, 1905). In nocturnal mammals such as opossum similar temperature maxima occurs during the night (Morrison, 1946). The ability to regulate body temperature varies also with age, maturity metabolic state and other factors (Prosser, 1952a).

Body temperature of the birds, is higher than that of the mammals, and "higher" mammals have higher temperature and better regulation than more primitive orders (Wislocki, 1933). During normal activity the more primitive mammals have lower body temperature than do higher mammals, and their temperature, although well above that of the environment, fluctuates with air temperature. The poorly regulating lower mammals are heterothermic. Bats, sloths and opossums show temperature fluctuation with the environment. Perhaps all of the heterothermic mammals readily enter a state of cold
The function of temperature regulation is not completely developed at birth, nor is that of the adult free from considerable limitations. The progress of its development in children, as shown by an increasing constancy in the diurnal cycle has been studied by Kleitman et al (1937). It was concluded from observations on decorticated dogs made by Kleitman and Camille (1932) that diurnal cycle of sleep and wakefulness is an individually acquired phenomenon depending upon the cerebral cortex for its establishment and maintenance. It was reported that it runs parallel with the diurnal body temperature curve (Kleitman and Doktorsky, 1933) and diurnal variations in steadiness and performance of muscular and mental tasks (Kleitman, 1933; Kleitman et al, 1935). Available data show that the newborn exhibits a daily variation in temperature, sometimes amounting to over one-half a degree centigrade. The first systematic study regarding this was made by Jundell (1904) who found that diurnal temperature range increased with age. Kleitman et al (1937) demonstrated a gradual increase in the regularity of the diurnal cycle and decrease in its range of temperature during the first year, leading to a definite establishment in the second year. From the studies of Vander Bogert and Moraves (1937) it is clear that development of temperature regulation continues for several years. In the hedgehog full development takes 31 days (Eisentraut, 1935). Gulick (1937) reported that a rat six days old at rest in a glass chamber jacketed by a waterbath at any temperature between 24°C and 37°C, quickly acquires a rectal temperature approximately 1.3°C to 1.8°C higher than the air of the chamber and if chilled for an hour or more to 20°C or lower, the rectal temperature drops to less than 0.5°C above the air of the chamber. At sixteen days the rats have a considerable degree of temperature regulation.
while muscularly active.

According to Buchanan and Hill (1947) development of temperature regulation may be correlated with development of myelination in nerve fibres in hypothalamus. A two-day old mouse is essentially a poikilothermic animal (Stier and Pincus, 1928); at 10 days a mouse regulates in intermediate air temperatures, and at 20 days in extreme temperatures. Development of temperature regulation in man may take several years (Burton, 1939).

Temperature regulation is perfected in chickens four or five days after hatching. Romanoff and Sochen (1936) and Romanoff (1941) demonstrated that the chick embryo is poikilothermic during early development, but it reaches true homoiothermism four or five days after hatching. Temperature regulation in the house wren appears gradually during the two weeks after hatching. Randall (1943) has demonstrated that the chick is capable of panting and shivering at or shortly after hatching, but until several days of post-hatching development neither mechanism is efficient in maintaining body temperature. In pigeons neither the panting threshold nor thermal tolerance is altered at high temperatures and humidity, but severe hyperthermia is rapidly developed (Randall, 1943).

It is generally recognised that tremors are important in temperature regulation of homoiothermic animals. Studies of Odum (1942) show that the development of co-ordinated muscle tremors corresponds closely with the development of temperature regulation in the small altricial species - the house wren and black-capped chickadee. No tremors were recorded from newly hatched and 3-day nestling which are poikilothermic but were present at all later ages roughly corresponding to the development of homoiothermy and inversely related to the air temperature.
A delicate balance between heat production and heat loss must involve in condition of homoiothermy. According to the prevailing physical conditions, the rate of heat loss by an animal may vary between wide limits. Similarly, the heat production, at least when the animal is exercising, must vary too. It is supposed that to meet the demands of any situation the balance between heat production and heat loss is achieved by independent variations in both these quantities. The polar fox normally existing at an environmental temperature some 60° below the temperature of its blood, can live in a temperate climate where the difference of temperature may be less than 20°C (Dawson, 1954a). If the animal could modify its heat production and heat loss, this adaptation to a changed environmental temperature could be more efficient and this is generally true of all homoiotherms although the relative importance of chemical regulation of heat production and physical regulation of heat loss, varies with different species.

An important factor in heat loss is a temperature higher than that of the environment, since it may be dissipated by convection and radiation; hence a resting animal, if it has a temperature above that of the environment, has a better chance of maintaining a constant temperature. The heat production may also be higher because of the more efficient method of heat dissipation. Moreover, the heat loss, with a temperature above that of the environment, may be regulated by the diversion of blood into the peripheral region which must necessarily have a lower temperature. In maintaining a high potential of vital activity and in permitting the regulation of heat loss, a high blood temperature is of great value. It is probable that a limit to the height of blood temperature is imposed by the requirements of heat production, so that a balance must be struck between the demand for a high temperature in the interests of temperature regulation and vital activity and a low
Thermoregulating Centre

It is now almost universally accepted and established that a "physiological centre" situated in the hypothalamic region is essential to the regulation of body temperature. Thauer and Peters (1937a, 1937b) and Thauer (1935), however, claim that after section of the brain stem of rabbits just behind the hypothalamus, after complete extirpation of the mid brain or lower transection of the spinal cord "a high degree" of thermal regulation persists in chronic preparations. Thus they conclude that the brain centre is not essential and that the peripheral nervous system must be capable of assuming to some extent the functions of temperature regulation. It is found by Issekutz (1937) and Issekutz et al (1937) that transection of the cervical cord in dogs decreases the resistance to cold. The thyroid gland was shown to play a role in the restoration of partial regulation in operated animals.

The importance of brain centre in the temperature regulation is not minimised by the existence of several subsidiary temperature regulating mechanisms including the adrenal and thyroid glands and control of metabolism by metabolic products. According to Frazier and co-workers (1936) the centre is located in the mesial hypothalamic nucleus of the cat and in the substantia grisea in man, close to the floor of the third ventricle. Later works indicate the existence of centres for heat loss and heat production in the cat. It has been shown that lesions in the anterior part of the nucleus have no effect on the resistance to cold but there is impairment in the resistance to heat (Ranson and Mague, 1936).
Same differentiation was also found in the monkey (Hanson et al, 1937). Differences in autonomic and motor localization have been shown by ectors et al (1938) and Grouch and Elliott (1956) by electrical stimulation of the hypothalamic centres. It has been demonstrated by Magoun et al (1938) that the effective region is the medial portion of the caudal part of the ventral telinephalon. It has been shown that in the goat stimulation of the "heat loss centre" between anterior commissure and optic chiasma causes polypnea, cutaneous vasodilatation and inhibition of shivering (Anderson et al, 1956). By electrical stimulation of the septal area, medial and dorsal to the heat loss centre, cold defense reactions could be elicited (Anderson, 1957).

It is well known that other parts of the brain may influence temperature regulation. Six cases of prolonged fever, without complications, following removal of the cerebellum was reported by Erlich (1937). Pinkston and Ricoh (1938) demonstrated that cortical areas 4 and 6 are important in vasomotor control. Decerebrate and spinal animals are unable to show temperature regulation.

Thermoreceptors and Sensation

The mechanisms of heat regulation are activated in two ways - by thermal receptors in the skin, and by direct stimulation of the thermoregulatory centre by changes in blood temperature. The peripheral thermoreceptors may elicit vasomotor reflexes even though the individual is not aware of heat or cold sensation. Observations of Bazett et al (1930) on man show that the bulbs of Krause, located at the outer border of the skin-layer containing blood vessels at a depth of about 0.1 mm, are probably
the cold-receptors, whereas the warmth receptors are the Ruffini organs, which lie deeper (0.33 mm) in the skin, where blood vessels are abundant.

Oppel and Hardy (1937) with their studies of the sensitivity of the peripheral heat and cold-receptors have shown that radiations of different wave lengths are effective in producing temperature sensation only in proportion to their absorption by the skin.

According to Sinclair (1955), in man temperature and other sensations are elicited from skin areas where no organised endings of any kind can be found. The same holds true for the tongue of the cat (Henseel, 1959). Although thermal and mechanical impulse discharges are recorded from this area, Kantner (1957) noted only the presence of a network of free nerve endings. It is agreed that a steady discharge frequency that depends on the absolute temperature is exhibited from the cold receptors in the tongue. The discharge is inhibited by hypoxia (Henseel, 1953), increased CO₂ concentration (Döct, 1956-57; Boman et al, 1957) and efferent stimulation of the lingual nerve (Döct and Walther, 1957) causing vasomotor changes.

In rats, cats and dogs cold receptor discharges from the external skin have been reported (Witt, 1958; Maruhashi et al, 1952; Boman, 1958). It has been found by Iggo (1958) that single C fibre preparations responded to noxious stimuli on the skin as well as to temperature changes and to light touch.

Cold Stress

Bartlett et al (1956) found that at higher muscular activity the temperature drop in restrained rats was more pronounced. Steen (1957) studied the adjustment of food intake to cold in pigeons. Masoro et al (1968, 1957a) using C¹⁴ incorporation into fatty acids found a high lipogenesis from
carbohydrate in the cold.

131 uptake by the thyroid in the cold in restrained rats is higher than in normal animals (Bartlett, Jr. 1957). Cold of 10°C increases 131 output from the thyroid gland of the rat, but at 2°C a depression of thyroid activity takes place (Brown-Grant, 1956). It has been shown by Arimura et al. (1956) that posterior pituitary hormones depress the increased thyroid activity in the cold. Administration of thyroxine in the rat was found to increase basal metabolism at 29°C, but not to stimulate the metabolic response to cold (Andlik et al., 1955). Swanson (1957) has observed a significant decrease of blood protein-bound iodine and of the epinephrine-potentiating effect of thyroxine in the cold.

The stimulation of adrenocortical function is apparently transient in nature and varies widely with species (Boulouard, 1957). Exposure of dogs for some hours to extreme cold resulted in increased output of steroid from the lumbo-adrenal vein which returned to normal values within 1 to 3 hours (Egdahl and Richards, 1956).

**Heat Stress**

In guinea pigs heat tolerance varies inversely with body size, probably an effect of surface-volume ratio (Wilber, 1957). From experiments with hypothalamic lesions Dohhoffer et al. (1957) have demonstrated that in the hyperthermic rat the increase in metabolism is of central nervous origin and not a direct effect of temperature on peripheral tissue metabolism. Acute hyperthermia increases plasma levels of 17-hydroxy corticosteroids in the dog from 4 to 15 μg./per cent or more (Barlow et al. 1956). Increase of corticoids during heating is abolished by hypophysectomy. A decrease in inorganic phosphate in plasma and urine at high environmental temperatures.
has been reported in dogs (Kanter and Lubinski, 1955). A marked reduction in the excretion of water in the normal rats was noted on heat exposure (Itoh, 1957).

**Acclimatization**

The basic processes inducing acclimatization remain obscure. Adaptations are thought to be superimpositions or modifications of more stable regulating mechanisms.

Small mammals in the tropics have critical temperatures of about 27°C, whereas those of birds range between 24°C and 20°C (Enger, 1957). Without water supply camels are able to tolerate 17 days in the heat. Schmidt-Nielsen et al (1956) have demonstrated that this is achieved by a dehydration tolerance amounting to 30%, low water loss by urine and feces as well as by evaporation, and tolerance to high body temperature.

**Cold Acclimatization**

Adjustment to cold in animals are achieved predominantly by changes of metabolism and overall insulation. Cold acclimatization reduces rapid reactions to acute cold stress, e.g., oxidation of C¹⁴ glucose (Depocas et al, 1957) or incorporation of F³² in the adrenals (Micholls and Rossiter, 1956). Bannom (1958a, 1958b) reported increased respiration of liver tissue of rats exposed to cold for four weeks, but after nine weeks of cold acclimatization no increase was found. During prolonged cold exposure hepatic lipogenesis is depressed (Masoro et al, 1957b). The incidence of ventricular fibrillation in hypothermia to drop from 96 to 9 per cent was found by Covino and Beavers (1957) in dogs which had been kept previously for one to four weeks in the cold; deacclimatization is accomplished after five days.
Iampietro et al (1957) reported that in man living in a cold climate has little or no effect on the diurnal pattern of rectal temperature. Using I131 uptake, Rodahl and Bang (1957) did not find any sign of increased thyroid activity in man exposed to cold. In the cold cutaneous blood flow and metabolism is higher in cold acclimatized subjects than in controls (Scholander et al, 1958; Elsner, 1955).

There is much evidence of the role of the thyroid in the adaptation to cold climate in rats. After a sojourn in the cold, the basal metabolism of rats is markedly increased (Schwabe and Emery, 1937; Schwabe et al, 1938). Chevillard et al (1957) have noted an increase in the weight of the liver of mice exposed to cold and an effect upon the islets of Langerhans has been reported by Simpson (1937).

Heat Acclimatization

Young and Cook (1955) observed that the melting point of body fat, but not of cutaneous fat, rises with high environmental temperature. Anoxic resistance is increased in heat acclimatization in mice (Hestand et al, 1955). In the heat acclimatized rat a doubling of antidiuretic substances are found by Robinson and MacFarlane (1956), and histological changes in hypothalamic nuclei and in the posterior pituitary lobes were noted by Usno (1957) in rats exposed to heat and cold. Hillermann and Wilson (1955) demonstrated that heat adjustment of body temperature in the chicken requires three to five days while respiratory frequency is acclimatized after eight to ten days.

Acclimatization to heat has been studied chiefly in man. There exists no essential difference in heat tolerance between Bushman and acclimatized Europeans (Wynham et al, 1956). Robinson et al (1955) demonstrated a reduction of 17-ketosteroid output in the spring as compared with the summer, Bass et al (1958) showed that there was no alteration in plasma, blood and circulating
Physical Thermoregulation

Physical thermoregulation means the mechanisms available to the animal for modifying the heat loss. There are three main channels, namely, radiation, convection and evaporation, by which the body accomplishes its loss of heat. Radiation may be defined as the transfer of energy from the surface of the body by electromagnetic waves. Under ordinary circumstances about 60% of total thermal loss from the body is achieved by this means. Amount of radiation depends on the difference between the temperature of the surface of the body and that of its surroundings and on the extent of the body's effective radiating surface. The skin of the body, the source of radiation, is the most important organ in any consideration of loss of heat. The blood supply to the skin is abundant and is under control of the central nervous system. The thermoreceptors of the skin receive sensations for heat and cold and transmit them to the cord and brain. Changes in ambient temperature have local effects in modifying circulation of blood through the action of peripheral vascular systems which are abundant in the extremities. There may be direct action of heat and cold on the walls of the blood vessels or they may act through chemical substances, such as acetylcholine. They may function through axon reflexes (Glasser, 1951). Through the sensory nerves there is also pathway to the spinal cord and through the sympathetic nerves back to the blood vessels. Heat regulating centre is situated in the hypothalamus. Production or loss of heat involves several different parts of the central and peripheral nervous systems.

The initial responses to changes in ambient temperature are local vascular reactions. In higher air temperature there is dilatation of skin
vessels and blood leaves the viscera and in low environmental temperature the reverse reactions occur. Retention of heat and heat loss is regulated by blood through the transfer of heat to the body surface. The characteristic of the peripheral tissues that permits them to lose heat through the skin surface is described as the skin conductance and it varies under different conditions according as the body must retain or lose heat to maintain thermal equilibrium. At low temperatures loss of heat by radiation exceeds loss by vaporization, but at higher temperatures there is predominance of loss by vaporization. Water is vaporized over three channels:

(i) by the sweat gland,
(ii) in the respiratory tract, and,
(iii) by insensible loss directly from tissue spaces and out of the skin.

Dubois (1939) showed that man loses about 20% of his heat by vaporization under basal conditions and the loss is 75-80% under exercise. In the birds, since they have no sweat glands and since feathers prevent much evaporation from the skin, the burden of heat loss falls mostly upon respiration (Randall, 1943). Randall studied the effects of varying humidity upon the ability of birds to adequately control the body temperature. He showed that when both environmental temperature and relative humidity was increased, there was no marked change in the panting threshold, nor there was any significant alteration in thermal tolerance. However, birds' ability to prevent a rapid rise in body temperature was inhibited. The efficiency of panting mechanism was decidedly less than normal due to decreased evaporation of water. Baldwin and Kendeigh (1932) pointed out that the mass or size of the body of birds is increased proportionately faster than does surface area and as a result more protoplasmic tissue is involved in heat production with comparatively little change in area for dissipation of heat.
Loss of heat by radiation and conduction is prevented by insulation. Aquatic mammals, most of which are hairless, have an insulating layer of fat. Molnar (1946) reported that heat loss in water by terrestrial mammals, man, dog and others, is twice as great as it is in air. Birds residing permanently in cold areas have a thicker feather cover in winter than do migrants to warm climates, and mammals have thicker fur coats in winter than in summer. The rate of loss of heat is reduced in case the depth of the temperature gradient between skin and ambient air is increased by fluffing up the hair or feathers in animals with hairy or feathered coat. Baldwin and Kendeigh (1932) caused a bird to go into hypothermia at an air temperature of 10°C by preventing it from fluffing its feathers, whereas it normally supported much lower temperatures. Giaja (1938) showed that in the pigeon, similarly restricted, more chemical regulation was required to combat the cold as its means of physical regulation were confined.

According to Duthie and Mackay (1940) heat loss by vaporization is increased when the body temperature rises above the "optimum" at a given humidity and air temperature. Sweat glands are stimulated and in animals lacking sweat gland and in birds panting appears. In dogs panting appears at rectal temperatures a few tenths of a degree above the basal rectal temperature (Hemingway, 1938). If allowed plenty of water for perspiration man can withstand very high temperature (Adolph, 1947). Vaporization occurring as air passes through the air sacs may have a cooling effect in birds.

When the body temperature is cooled below "optimum", shivering may begin, which is associated with vasoconstriction and piloerection. It is reported that the abilities to pant and shiver develop in the young animal during the period when temperature regulation appears (Odum, 1942; Randall, 1943).
Chemical Temperature Regulation

In considering physical thermoregulation the emphasis has naturally been on heat loss; by chemical temperature regulation we mean the increase in heat production of an animal in response to cold. The homoiotherms respond to a lowering of its environmental temperature by an increase in heat production. As air temperature becomes lower or higher the metabolism remains constant, while the physical insulating mechanisms compensate for the changes in heat loss. The physical insulating mechanisms in thermal loss are finally insufficient, and at elevated blood temperature metabolic rate rises according to tissue temperature, but at lowered blood temperature there is activation of muscular movement as shivering, due to the stimulation of the thermoregulating centre and increase in tissue metabolism (thermo-genesis) probably as a result of secretion of endoerins. Thus in a range of thermal neutrality the metabolism of homoiotherms is minimal and increases both above and below this range, whereas in poikilotherms metabolism varies directly with temperature.

It has been suggested that shivering can be elicited from cutaneous receptors alone. This conclusion is drawn from experiments with man and animals (Good and Sellers, 1957a, 1957b; Horvath et al, 1955-56; Spurr et al, 1957) showing a rapid onset of shivering in the cold without any drop, or even with a slight increase, in rectal temperature. Shivering is inhibited by hypoxia (Hemingway, 1955-56), carbon dioxide and intravenous epinephrine (Good and Sellers, 1957b). The effectiveness of shivering to compensate heat loss depends largely on the mass of shivering muscles, as, for example, in the pigeon, where the big pectoral muscles are important heat source in the cold (Steen and Eager, 1957).

Chemical thermogenesis contributes to a considerable degree to total heat production of rats in the cold. Donhoffer et al (1957a, 1957b) noted
a periodic increase in oxygen consumption with a coincident drop in muscle temperature and a rise in abdominal temperature. Davis and Mayer (1955) estimated the chemical thermogenesis in the curarised rat to be about 40% of the metabolic increase in the cold. In stimulating chemical heat production the adrenergic system plays an important role (Heisch et al., 1957a, 1957b).

In the metabolic response to lower temperature there is much species variation. Rendeigh (1944) reported that for air temperatures from 0-37°C the body temperatures of English sparrow was 41.5°C, but the heat produced per gram per hour at 37°C was one half the amount produced at 0°C. Above 37°C there was somewhat increase in body temperature and the heat production increased more. It has been shown that heat production of two species of birds, the goose and Melopsittacus, increases when proceeded from a moderate to lower temperature (Dawson, 1954b). The response of thermogenesis is much less pronounced in goose, which is well protected by its down against heat loss, than that of Melopsittacus which is poorly provided with insulation and rely more heavily on chemical regulation for maintaining a constant blood temperature. In the mammals, on cold exposure, there is increased liberation of epinephrine, adrenal corticoids and thyroid hormone and as a result metabolism is increased. It has been reported by Brobeck (1946) that adrenalectomized or thyroidectomized rats lose ability to compensate for cold.

Arctic birds and mammals have better insulating ability than tropical species. In the arctic fox air temperature can be lowered to -30°C without any increase in metabolism. In the Alaskan ground squirrel cold stress of -10°C, however, is sufficient to elicit a rise in metabolism (Prosser, 1952a). In well acclimatized birds and mammals of the arctic heat production is increased by a small amount as the ambient temperature falls, while the
metabolic increase is much greater in tropical species.

A basic condition for homoiothermism is high basal metabolic rate. Heat production may be measured by direct calorimetry or from a number of bodily functions, such as oxygen consumption, carbon dioxide elimination and insensible perspiration, which, under controlled conditions, are sufficiently proportional to heat production to serve as measures thereof. When determined both for animals within a given species and for those of closely related phylogenetic groups, oxygen consumption for small organisms have higher rates of oxygen consumption than larger organisms. Studies of the metabolism of some of the smallest mammals, by Morrison (1948) and Pearson (1948), give additional evidence for the general rule relating gas exchange to size. The asymptotic increase in metabolic rate with decreasing size places the lower limit of size for mammals at about 2.5 g. A smaller mammal would be unable to obtain adequate food for its infinitely rapid metabolism. Studies of oxygen consumption on arctic, temperate and tropical mammals indicate that the metabolic regulation may be in part a function of the insulation efficiency of the body surface (Bishop, 1952). The basal metabolic rate is higher in individual mammals adapted to a cold environment than in warm-adopted individuals. It has been noted that the period of maximal basal heat production in birds occurs fifteen days after hatching, a period which corresponds closely with the attainment of adult body temperature levels (Randall, 1943).