

THE DEVELOPMENT OF TEMPERATURE REGULATION IN THE OPOSSUM, DIDELPHIS MARSUPIALIS VIRGINIANA¹

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THE development of the ability to maintain normal body temperature depends upon the development of a variety of factors that modify heat dissipation and heat production. However, before these factors can be considered individually it is desirable to evaluate their combined effect in resisting cold stress. Some animals are *precocial* and, almost from birth, are able to regulate their body temperature. Others, such as the white rat and hamster (Buchanan and Hill, 1947, 1949), and the red-backed mouse (Morrison *et al.*, 1954), classed as *altricial*, are bare and helpless at birth and require a period of protected development before regulation is achieved. This delayed development of regulation provides an opportunity for measurement of the various factors necessary to its attainment.

The opossum is not only altricial but undergoes the major portion of its development within the marsupium after a gestation period of only 13 days (Reynolds, 1952). The young are easily removed from the pouch for study as early as 30–40 days of age. As the only marsupial in the fauna of the United States, the opossum is our most primitive mammal. Its skeleton, at least, has changed but little in the last 80 million years (Dobshansky, 1955) and so it may represent one of the earliest homeotherms.

This paper will describe the development of temperature regulation in terms of the ability to maintain the body tem-

perature at various ages. However, one cannot simply state that an animal is either a regulator or a non-regulator since even the most effective homeotherm has its limits in both range and precision of regulation. Both the variability of the body temperature (T_B) and the level of ambient temperature (T_A) must be considered. In general, two categories of factors interact to produce body temperature. First, the activities of a regulatory mechanism, including sensing, integrating, and effector systems, will be reflected in the constancy of body temperature. And second, those physical and "chemical" factors concerned with the capacity to regulate will set the limits of effective regulation. Because the rates of development of these factors may be different, careful selection of the experimental T_A is necessary. For example, if the capacity to produce heat or to limit its loss is very small, then at a low T_A there is little evidence of a regulatory mechanism because of the insignificant temperature differential ($\Delta T = T_B - T_A$). However, at a milder T_A significant differentials may be maintained. Comparison of these differentials over a T_A spectrum allows characterization of the regulatory mechanism.

The simple relations between T_B and T_A during development describe the *sum* of temperature regulatory activities and allow some useful conclusions to be drawn concerning the capacity to regulate and the characteristics of the regulatory mechanism. This paper is concerned with this over-all description and those deductions regarding regulatory func-

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tions which may be drawn from it. Subsequent papers will consider the measured characteristics of these various physical and physiological factors in the opossum.

MATERIAL AND METHODS

Female opossums with pouch-young were obtained through trapping operations near Madison, Wisconsin, or from commercial sources in Kansas and Florida. The animals from Florida represented a different subspecies (*Didelphis marsupialis pigra*), but supplied only a small

plements of fruit. Data gathered over four years were obtained from some two hundred animals and twenty-six litters as follows: 20 (3) in 1954, 71 (7) in 1956, 49 (5) in 1957, and 62 (11) in 1958.

Method of aging.—The young were received at various ages ranging from 30 to 60 days, so the method of aging was of the greatest importance if a chronology was to be established. The head-body length of each animal was determined as early as possible and thereafter other values were taken whenever the animal

TABLE 1

VARIABILITY OF BODY LENGTH IN OPOSSUMS OF SEVERAL AGE CLASSES

Age (Days)	Length (Mm.)	Standard Deviation (Mm.)	Coefficient of Variation (%)	Time Equivalent (Days)
55.....	82	3.5	4.2	1.5
65.....	106	3.3	2.9	1.3
75.....	135	5.5	4.1	1.8
85.....	168	6.4	3.8	2.0

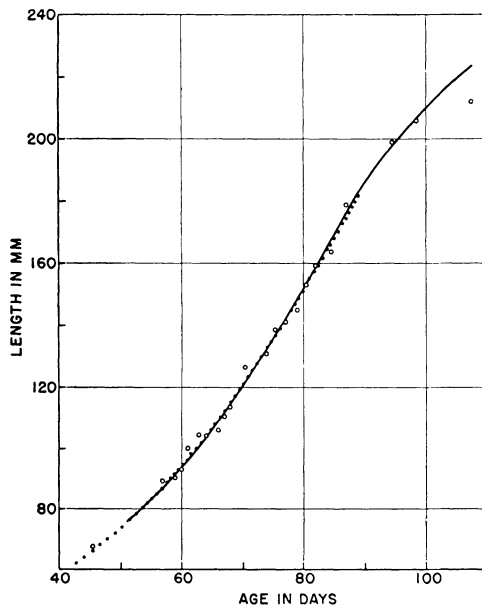


FIG. 1.—Growth curve showing length as function of age. Solid curve represents best fit through open circles which are mean values by age classes (average $n = 13$). Points show reference data from Hartman (1938) and Reynolds (1952). Early growth rate equals 3.1 per cent/day.

fraction of the data (*ca.* 2 per cent). All of the other animals were *D. marsupialis virginiana* (= *D. virginiana*), the subspecies studied by both Hartman (1928) and Reynolds (1952). They were caged individually and fed on rat chow and white rat carcasses with occasional sup-

plements of fruit. From these values a curve of length versus age was constructed for each litter. The best fit of these curves to a standard curve of length versus true age (Reynolds, 1952; Hartman, 1928) was utilized to determine the birth date of each litter (Fig. 1).

The accuracy of this age estimate is related to the reliability of the reference data. The data of Reynolds and Hartman agree closely although derived from Californian and eastern material, respectively, and consist of large samples. (Reynolds studied 161 individuals from 25 litters.) The range of length at any given age is two- to threefold greater in the reference data than in this study. The difference in the size of the samples may account for this difference in range. Since our age estimates were each based on measurements of a whole litter (6–12) the uncertainty on any given date should be about one-third that shown in Table 1 for individual values or less than one day.

The form of the growth curve was exponential and similar to embryonic and early growth curves for other organisms (Brody, 1945). If the logarithm of length (L) in millimeters is plotted against the age (A) in days, a linear curve is obtained below 90 days: $A = 9.0 \log L - 12.1$. The maximum rate of growth, about 4 mm/day, occurs between 80 and 90 days at the inflection point between the exponential and self-limiting phases.

Cold exposure and body temperature measurement.—Battery jars ($8 \times 12 \times 8$ inches) with lead ballast and fiberboard covers were immersed in constant temperature baths. The animals were held in wire cages just large enough to allow curling and adjustment of position, and mounted on wooden blocks one inch off the chamber floor. The T_A was selected to apply a stress only moderately beyond the capacity to regulate in order to provide the maximum measurable effect, since stresses far exceeding the capacity to regulate may induce a maximal physiological response but result in small values for ΔT . The T_A was successively lowered as the regulatory capacity increased.

The T_B and T_A were recorded at half-minute intervals to within 0.2°C . with iron-constantan thermocouples and a Leeds-Northrup recording potentiometer. Thermocouples ranged from 30 to 18 gauge depending on the size of the animal. The thermocouple was inserted rectally into the inner core of constant T_B (beneath the inferior margin of the liver), a distance varying from 1 cm. in very small animals to 15 cm. in the largest. Little trouble was encountered with animals removing the thermocouple which was secured to the tail with adhesive. Any variable insertion of the thermocouple caused by activity was controlled by careful check of the depth of the in-

sertion at the end of the experiment. A few cases with an irregular T_B due to slipping of the thermocouple were discarded.

The initial T_B was recorded immediately on removal of the subject from the pouch after which a continuous record was obtained and an equilibrium T_B , defined as one not falling by more than 0.2°C . in 15 minutes ($<1^\circ/\text{hr}$), was determined. In some very small animals in which the T_B can fall to within 0.5°C . of the T_A , the experiment was interrupted before this low point was reached. In others, a gradual drop of T_B (ca. $1.0^\circ/\text{hr}$) was observed after the major drop had occurred. In this case, the actual equilibrium T_B was never achieved, and the values were recorded as being slightly higher than the true equilibrium value.

An equilibrium T_B , usually achieved in about two hours, was obtained for animals ranging in age from 57 to 100 days and at T_A of 5° , 10° , 15° , 21° , 24° , 27° , and $30^\circ \pm 1.5^\circ \text{C}$. In early stages of regulation, when the T_B was close to the T_A , the ΔT ($T_B - T_A$) was the important consideration. Accordingly, a T_B measured at a T_A slightly different from the class value (e.g., 26° vs. 27°) was adjusted by this difference (i.e., -1°). In the later stages of regulation, differences of a degree or two had little effect on the large ΔT values, so the T_B values close to the adult level were not adjusted.

Effort was made to randomize the selection of animals, in order to avoid the effects of variation in nutrition, and such factors as the mother's response to confinement which in certain instances caused her to kill or neglect her entire litter. To minimize the effects of adaptation or injury, as much time as possible, usually about 5 days, was allowed to elapse between successive experiments on any individual. The T_B in several animals at 60 to 70 days of age fell to $3\text{--}5^\circ \text{C}$.

and remained there for periods up to several hours, but these animals subsequently showed no ill effects.

RESULTS

These experiments were designed, first, to identify the presence of regulation as soon as it appeared; next, to evaluate the capacity to resist temperature stress; and finally, by presenting various degrees of stress, to indicate the adequate stimulus to regulation. The primary unit of data is the cooling curve. Such curves describe the change in T_B with time after transferral to an experimental T_A . Figures 2 and 3 show repre-

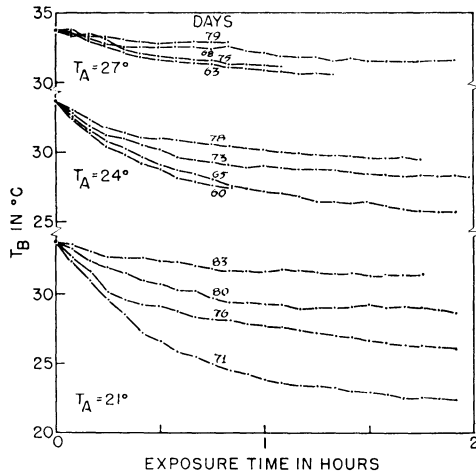


FIG. 2.—Representative cooling curves at ambient temperatures (T_A) of 27°, 24°, and 21° C.; age in days as indicated.

sentative cooling curves at various ages and illustrate the rapid fall of T_B in younger animals. Initial body temperature varied less than 2° C. from the average adult value of $35.2^\circ \pm 1.2^\circ$. As the developing animal becomes better able to regulate, the cooling curve approaches a horizontal line (Fig. 2).

Several values may be taken from these curves: (1) The equilibrium T_B at which heat production equals heat loss; (2) the equilibrium ΔT ; (3) the rate of

change of body temperature (dT_B/dt) at specified points along the cooling curve (0, 15, 30 min.); (4) the cooling constant at these times, which is the rate of change of body temperature per unit temperature differential ($dT_B/\Delta T dt$).

In Figure 4 equilibrium T_B values are plotted against age at two representative values of T_A . Differences in adaptive responses to the stress, such as shivering and curling, as well as maladaptive responses such as struggling and licking of extremities when exposed to cold con-

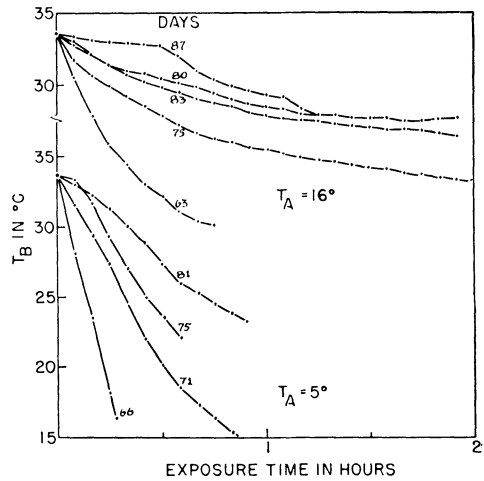


FIG. 3.—Representative cooling curves at ambient temperatures (T_A) of 16° and 5° C.; age in days as indicated.

stitute by far the major sources of variation. Some idea of the importance of such a factor as curling can be seen from the two points for litter mates at 75 days and 24° C. connected by a dotted line in Figure 4. The upper point represents a curled animal and that below, an uncurled animal. The presence of shivering contributes a highly variable influence because of its intermittent nature during exposure to cold and of its presence in some litters and not in others of the same age. Excitement caused inefficiency in temperature regulation, so that animals struggling to free themselves always at-

tained a T_B well below the range of quiet animals. T_A values below 16° caused more disturbance than those above and were reflected in a greater variability. Immediately previous exposures to heat were found to alter the subsequent response to cold. For example, two 80-day animals placed at 18° , after being heated to a T_B of 40° , regulated at a T_B of only 21.7° and 22° . Another, warmed to 37.4° had a similar T_B of 21.4° , all about

may be divided into three phases: (1) an initial gradual rise, (2) a rapid phase with an inflection seen more prominently at a lower T_A , and (3) another slow phase representing a final gradual attainment of adult T_B . That the regulation of T_B is relative to the T_A is clearly seen from these curves and in the continual lowering of the *critical temperature for regulation* which may be taken as the T_A at which the T_B can just be maintained

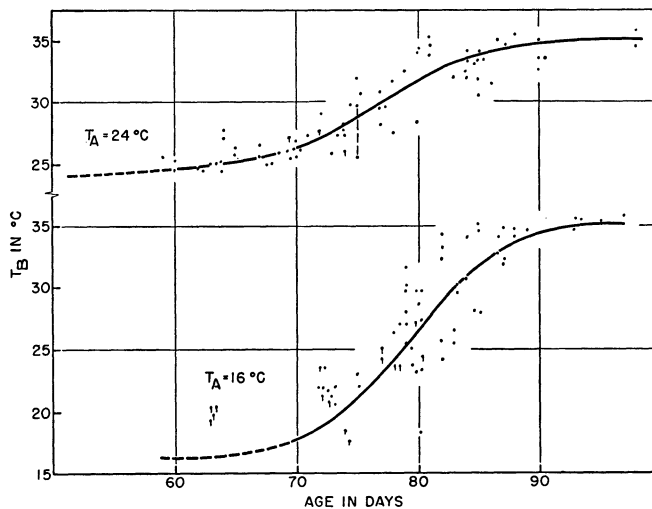


FIG. 4.—Equilibrium body temperatures (T_B) as a function of age at ambient temperatures (T_A) of 24° and 15° C. Average curve is drawn through means by age classes ($n = 2-6$). Tabs indicate non-equilibrium values. Points connected by a dotted line represent curled (*above*) and uncurled (*below*) litter mates.

5° below the mean for this age and T_A . All of these animals showed a licking response during exposure to heat. Residual moisture on the extremities may in part account for the differences in equilibrium body temperature, since animals with extremities inadvertently moistened from other causes show similar differences.

Figure 5 shows average T_B curves for all T_A values studied. The earliest signs of regulation were seen with the mildest stress of 30° C. At a lower T_A regulation was less effective. The sigmoidal curves

within two standard deviations of the adult mean, that is, above 32.5° .

Reynolds (1952) measured cooling curves at a single T_A of 13° C., on three animals each at 69, 75, 81, 87, and 94 days of age and recorded equilibrium values ($dT/dt < 1^\circ/\text{hr}$) at the latter three ages. His mean values are shown as crosses in Figure 5 and lie in a fairly appropriate relation to our curves for 16° and 10° .

DISCUSSION

While the curves in Figure 5 represent the most direct description of tempera-

ture regulation, they are not the most convenient form for analysis. Although the T_B will vary with the T_A in the young animal, we might expect the ΔT to be more constant since it represents the actual *degree of maintenance*, combining in a single term the metabolic (heat production) and conductance (heat dissipation) factors: $\Delta T = M/C$. These differentials are presented in Figure 6 as a function of age at various ambient temperatures.

duction. By taking the ΔT as directly proportional to the metabolic response, this response can be characterized at any *given age* and the variation in *response to* T_A of animals at various ages compared.

An example of this approach is shown in Figure 7, in which the ΔT values are shown as a function of T_A for animals at 5-day intervals. If insulation increases with age and the metabolism depends only upon T_B (Q_{10} effect), then the metabolism should decrease continuously

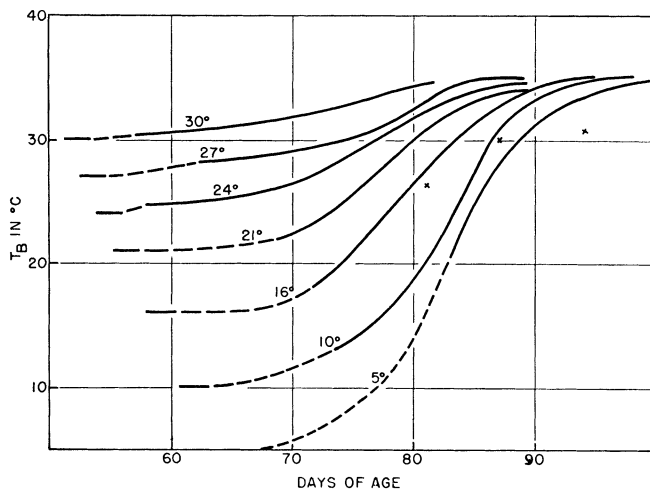


FIG. 5.—Mean curves for equilibrium temperatures (T_B) as function of age at indicated ambient temperatures (T_A) (cf. Fig. 4). Crosses show values from Reynolds (1952).

Two major factors—increasing insulation and maturation of the regulatory mechanism—must account for the greater ability to regulate in older animals. The data presented here represents the sum of these two factors and so their relative importance in animals of different age cannot be determined. Physical changes which result in increased insulation are not considered here. However, if one assumes that *at a particular age*, insulation remains nearly constant at various values of T_A then the differences seen in ΔT are related to differences in regulatory processes, that is, heat pro-

duction. This type of curve may occur below 60 days.

If there is increased insulation in older animals and constant metabolism at all T_A values, then a series of horizontal lines representing regulation at each successive age would result. This effect is seen at 60–75 days. Although the ΔT values were much alike, the T_B values represented by these curves vary by over 10° C. Because of this difference, a depression of metabolism due to the lower T_B was expected, but not seen. There was no Q_{10} effect, the heat flow being the same regardless of body temperature.

Such a response requires some stimulation of metabolism at a lower T_B even though metabolism is not yet adequate to maintain that T_B .

This effect was even more strikingly shown in older animals (70–90 days) in which the ΔT actually increased with decreasing T_A . But since there must be some limit to this metabolic stimulation, the curves will pass through a maximum with further decreases in T_A as the reduced T_B depresses the metabolism (Q_{10} effect). Regulation is still not achieved

at a mild T_A even though the required differential is less than that maintained in a colder environment. For example, at 80 days and $T_A = 27^\circ\text{C}$, $\Delta T = 5.5^\circ$; T_B has fallen by 2.5° to 32.5° . An 8° differential was required for maintenance but only 5.5° was produced. However, at $T_A = 21^\circ$, the $\Delta T = 8.8^\circ$ and at $T_A = 16^\circ$, $\Delta T_E = 10.2^\circ$. Accordingly, this animal had adequate capacity for complete regulation at 27° but this was not elicited. If marked changes in insulation or in effective surface area can be excluded,

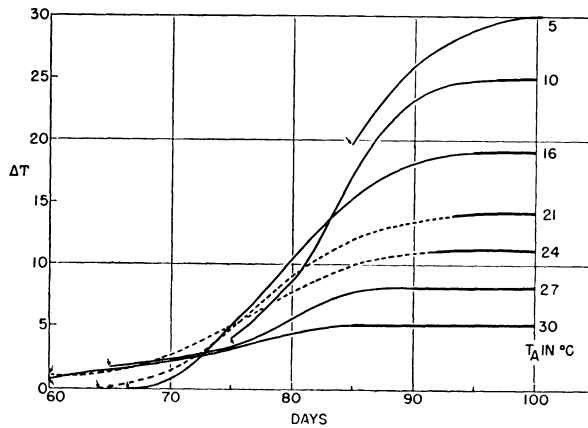


FIG. 6.—Equilibrium temperature differentials ($\Delta T_B = T_B - T_A$) as function of age at the indicated T_A . Dotted lines are present to assist in differentiating curves. Heavy sections represent complete regulation.

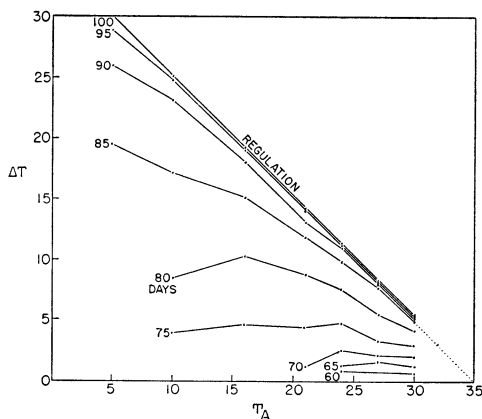


FIG. 7.—Temperature differentials (ΔT) as function of T_A at various ages as indicated. Limiting 45° slope represents complete regulation.

then the changes just described must represent changes in heat production.

The forms of these curves indicate that a feeble but adaptive metabolic response exists perhaps as early as 60 days and that from this age on, the metabolic response increases very rapidly. This metabolic response plus an increasingly effective insulation leads to eventual regulation at the T_A values studied.

In Figures 5, 6, and 7 there is some difficulty in comparing changes in regulation at different T_A values since the shape of each curve differs from the next. In Figure 8 an attempt is made to present regulation at different T_A values on

a common basis to include some expression of the intensity of the thermoregulatory load. Here regulation is expressed as the fraction of the adult ΔT attained ($T_B - T_A/35^\circ\text{C} - T_B$). These curves are quite similar, although not identical, in shape (except for 27°) and are displaced to the right as the T_A is lowered. "Horizontally" one may consider at what age a certain percentage of regulation exists; or, "vertically," how the per cent of regulation varies with T_A at any age.

the ΔT at a critical T_B of 32.5°C ., which is high enough so that we may consider function uninfluenced by falling T_B , and low enough (-2 standard deviations) so that we can be sure that regulation has been exceeded. In other words, this represents the maximum response (ΔT) of the animal while still within the normal T_B range and so may represent our most effective single criterion of (precision of) regulation. The rapid attainment of resistance between 80 and 90 days is clearly seen here. Actually, the relative effective-

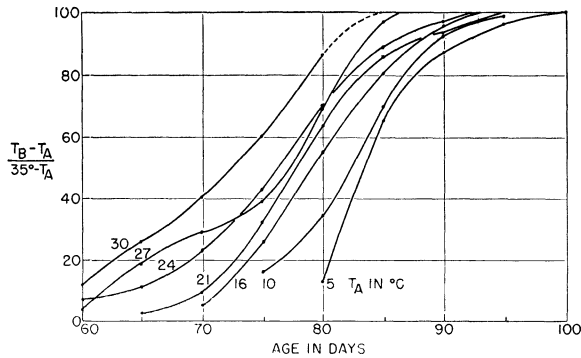


FIG. 8.—Degree of regulation in young opossums at various T_A as compared to adult ($T_B = 35^\circ\text{C}$.) expressed as ratio of equilibrium body-temperature differential to adult body-temperature differential or $(T_B - T_A)/(35^\circ - T_A)$.

The preceding grid allows one to compare other animals with some facility. Such a reference is very desirable if one is to compare development in heterogeneous material, and may be essential since the reference data is often fragmentary and relates to different stages of growth or different test conditions. Another useful index which can be expressed in absolute units is shown in Figure 9. Here the T_A at which a given fraction of complete regulation is achieved is plotted against age. The slopes of these curves which are substantially linear vary somewhat (2.0° – 3.0° /day) but give a mean value of 2.5° /day for the four "degrees" of regulation plotted.

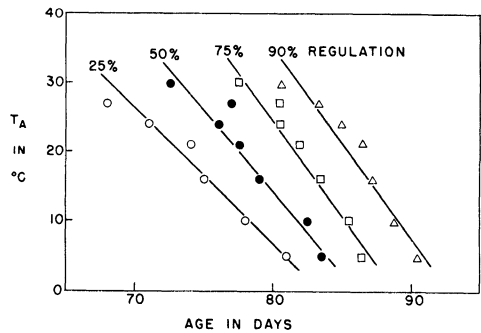


FIG. 9.—Relation between T_A and age at which various fractions of regulation are achieved ($T_B - T_A)/(35^\circ - T_A)$.

ness of the regulation is increasing at a constant rate (ca. 20 per cent/day) between 65 days, the beginning of demonstrable regulation, and 90 days as may

Figure 10 shows, as a function of age,

be shown by the linearity of a logarithmic plot of ΔT ($T_B = 32.5^\circ$) from Figure 9. Just above 90 days a sharp break appears in the curve which signals the end of the maturation phase of the regulatory mechanism. Regulation changes in older animals at a much slower rate (*ca.* 5 per cent/day). These rates of maturation correspond to those for other developmental factors including organ and body growth and metabolic changes (Meyer and Morrison, unpublished observa-

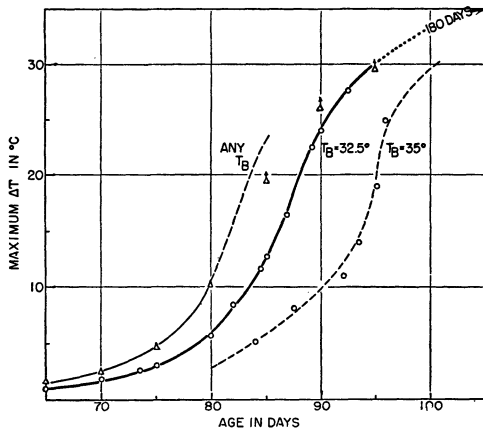


FIG. 10.—Maximum temperature differentials (ΔT) as function of age at $T_B = 35^\circ$ C. (adult level); at 32.5° C. (adult level — 2 standard deviations); and at any T_B value. Because of gradual attainment of adult level, age values in right-hand curve are more uncertain than others.

tions). A similar curve, placed with more uncertainty, is that for the ΔT at which a T_B of 35° , the mean adult value, can be maintained. Also shown in Figure 10 is a curve of the maximum ΔT occurring at any T_B . The displacement of this curve to the left shows differentials where regulation is not possible equal to those at an older age where regulation is possible. Since the T_A is lower in the former situation, the quality of regulation must be improving as well as the regulatory capacity. When and if complete control of the thermoregulatory potential is ob-

tained, these three curves should approach one another, but observations on 180-day animals still show a higher temperature differential at $T_B = 32.5^\circ$ ($\Delta T = 35^\circ$) than at 35° ($\Delta T = 30^\circ$).

Comment.—The regulatory processes may be divided into three categories: afferent or sensory activities, integrating activities, and effector activities. These will be subject to two types of influence which will govern their function; extrinsic influences, such as the stimulating effect of temperature upon a receptor or the arrival of impulses at an integrating center; and intrinsic influences, such as the effect of temperature upon the metabolism of any part, or the presence of intermediary metabolic factors in adequate amounts. At any stage in development these three activities must be considered both individually and in terms of their less obvious interactions.

Although several theories have been proposed, we do not know what constitutes the adequate stimulus for a temperature receptor. Experimentally it has been shown that the nerve fibers from temperature receptors respond to abrupt changes in temperature with a sharp rise in impulse frequency which is followed by a gradual fall to a new level when finally adapted. It is also known that the impulse frequency depends upon the temperature of the receptor and that various receptors have characteristic temperature functions in this regard depending upon whether they subservise sensations of heat or cold (Hensel, 1953). Histologically the presence of bare nerve endings which are believed to carry impulses for both pain and temperature suggest that when pain sensation is present, temperature sensation may also be present (Weddell *et al.*, 1955). Nociceptive stimulation of very young opossums (30–40 days) results in withdrawal of the part. If, on this basis, one could assume

the presence of temperature reception, then the low temperatures attained experimentally should certainly provide sufficient stimulation for a response. But the existence of temperature receptors does not insure adequate reception. The development of a more adequate response to the cold stress seen in the second phase of the curve in Figure 6 may in part be due to improved reception of the ambient temperature. An increase in the total number of impulses from temperature receptors, believed by many to be related to the magnitude of the regulatory response (Hensel, 1953) could be accomplished either by a change in individual receptor discharge or by a change in receptor distribution and density. The change in insulation over the skin as well as its thickness will also modify the receptor input. Teleologically, temperature reception may be of definite value even before metabolic alterations are possible if the animal is stimulated to move to a more favorable environment (behavioral regulation).

Even though adequate reception of temperature were present, the development of other components of the regulatory mechanism is still necessary before resistance to cold, which appears initially in the second phase of the curve in Figure 6, is possible. Maturation of integrative function may account for this improvement in regulation.

The spinal cord of the cat exhibits increased electrical activity when cooled as a result of decreased synaptic resistance (Suda *et al.*, 1957). This activity passes through a maximum with the tissue becoming inexcitable around 20° C. A similar phenomenon may be behind the hyperreactivity to tactile stimuli, increased deep tendon reflexes (clonus), coarse tremor of the head, etc., which are seen at low body temperature in the opossum. Such activity may in part account for the

T_B values seen at low T_A , but it seems more logical to relate the appearance of early regulation to the development of integrating centers which mediate more specifically the adaptive responses. In the very young opossum the threshold of these centers may be very high or their connection to peripheral receptors inadequate. With reduction in body temperature, receptor input increases and the threshold of the integrating center falls. As the capacity of the animal to produce heat and resist its loss increases with age, regulation becomes more adequate. At the same time, the sensitivity of the integrating center must increase, first, because central temperature is less likely to fall and, second, because relative receptor input may even become less as insulation increases. If the capacity to resist cold is exceeded and body temperature falls, then eventually the integrating center will come to a temperature below which its specific reflex activity ceases or it stops functioning altogether. Failure of the integrating center may account for the presence of maxima in the T_B curves in Figure 7. The shape of these curves and the presence of maxima predominantly in the 24°–27° C. range is very similar to those obtained for reflex activity in the spinal cord of the cat.

There is not sufficient information available to permit quantitation of the above factors. It is difficult to define a temperature receptor because the response of any nervous element is modified by a temperature change. In the end, a receptor benefits the animal only to the extent that it mediates adaptive responses. A reduction in the threshold of the integrating center which may occur with lowered body temperature would constitute a kind of deep temperature reception and provide for crude regulation. It is immaterial from the standpoint of definition whether or not this occurs by

means of specialized cells. Recent observations by Benzinger (1961) have shown the direct influence of blood temperature on regulation to heat in man. However, it by no means follows that regulation to cold must be controlled similarly. For example, in a number of small arctic species such as the red squirrel, the deep body temperature is no lower in the cold (to $-20^{\circ}\text{C}.$) and sometimes is actually higher (unpublished observations). Here, temperature receptors in the skin which encounter the temperature change must be the effective sensing device. The importance of reductions in brain temperature in modifying regulation and its role in a more primitive type of regulation is unknown. Recently attention has been drawn to this subject by Fusco *et al.* (1959) who investigated temperature gradients in the dog brain. Adolph (1951) has discussed the possibility of two barriers against cold, one central and the other peripheral.

The third category, effector activities (for cold regulation), represents primarily the muscles. Given a stimulus, several factors will determine the amount of heat production per contraction. The output will vary with the size of the fiber (muscle mass) and its myofibrillar content as well as with the rate of metabolic processes at work to restore potential energy after heat is released. In this regard the temperature coefficient of the tissue becomes important during regulation at reduced body temperatures. Indeed, the presence or acquisition of a heat-producing system with a low-temperature coefficient may be thought of as a kind of temperature regulation. And observations on tissue slices have shown just such a transition in heart, diaphragm, and skeletal muscle in the opossum. Between 50 and 85–105 days of age the Q_{10} changes from 2.1 to 1.2 (Meyer

and Morrison, unpublished observations).

Comparative aspects.—Since the opossum represents a primitive group of mammals it should be instructive to compare it to other forms. The marsupials, as a group, have somewhat lower mean body temperatures than many higher animals, but their ability to regulate against cold stress is well developed (Morrison, 1946). The opossum in particular survives winter conditions as far north as Vermont (Hamilton, 1958). Unfortunately, information on the development of temperature regulation in mammals is too limited for effective comparison. Development progresses more slowly in larger animals so the opossum should be compared to animals of comparable size. Similarly, a given temperature will represent a quite different cold stress in a large animal than a small one.

Of the species listed in Table 2, which summarizes development (of good resistance at 0° – $10^{\circ}\text{C}.$) in various animals, the cat (at 70 days), dog (at 70 days), rabbit (at 40 days), guinea pig (at 100 days), and porcupine at 115 days) are roughly equal in size, but only the latter two have “developmental times” comparable to the opossum (105 days). About the best that can be said is that these three rather unaggressive species are comparable in their limited abilities for “fight or flight” in contrast to the more effective dog, cat, and rabbit. The porcupine is of particular interest as a precocial form which regulates effectively at birth and thus develops temperature regulation entirely in the uterus. The opossum spends only one-eighth of its developmental period before birth, and yet the over-all developmental times needed to achieve regulation are almost the same.

Regulation in several of the smaller rodents is achieved within 40 days of total developmental time, but all activi-

ties are speeded up in these small animals which may have average life spans of only a year. Indeed it has been suggested, originally by Rubner, that the product of (specific) metabolic rate and life span in mammalian species of different size may be constant (Brody, 1945). This proposition will be difficult to prove because of the unreliability of information on life spans, but values from data recently compiled (Spector, 1956) are reasonably

the stage of temperature regulation) appears to require a larger fraction of the life span in this animal. This may represent a characteristic of, and a liability for, this primitive group of mammals (see Fig. 11).

SUMMARY

1. The development of temperature regulation in the opossum, *Didelphis marsupialis virginiana*, has been de-

TABLE 2
DEVELOPMENT OF COLD RESISTANCE IN YOUNG MAMMALS

SPECIES*	GOOD RESISTANCE AT		GESTATION †	TOTAL ([1]+[3])	SUMMED L O ₂ /Gm ‡
	0°-10° C.	15°-25° C.			
	(1)	(2)			
White mouse	20	(10)	18-20	39	1.39
Red-backed mouse	15		(20)	35	1.35
Syrian hamster	30-44		16	53	1.28
White rat	18-30		23	47	0.82
Hedgehog	31	31	34-49	73	1.32
Guinea pig	30		67-68	98	1.70
Cat		1-4	63	(70)	0.74
Rabbit		3	30-32	(40)	0.38
Opossum	90-95	85	13	105	2.14
Porcupine	3	3	112	115	1.65
Dog		4	58-63	(70)	0.50
Pig	10		112-15	124	0.50

* White mouse, Sumner (1913); red-backed mouse, Morrison *et al.* (1954); hamster, Buchanan and Hill (1949); rat, Buchanan and Hill (1947); hedgehog, Eisentraut (1935); guinea pig, Edwards (1836); cat, dog, and rabbit, Leichtentritt (1919); porcupine, Ryser (1952); pig, Newland *et al.* (1952).

† Days.

‡ Product of "development" time (col. [4]) and B.M.R. (adult).

described by the relation $S = CW^{0.27}$ which combines with the familiar relation for (weight specific) basal metabolic rate, $M = CW^{-2.7}$ to give a constant product $S \times M = C$ (= ca. 30 L O₂/gm). If we provisionally accept this proposition, then the duration of development can be expressed as a summed oxygen consumption which would represent a definite fraction of that volume corresponding to the life span. Such values in Table 2 (col. 5) bring the mice into reasonable agreement with the larger rodents. And they give the opossum the highest value; that is, development (to

described in terms of the equilibrium body temperature (deep rectal) as a function of age at ambient temperatures from 5° to 30° C. The earliest signs of regulation are seen at 30° ambient and 60 days of age. Lower ambient temperatures are associated with later regulation, until at 90 days of age an ambient temperature of 5° is withstood.

2. The immature animal may demonstrate adequate regulatory capacity which is not utilized, since greater regulation—expressed as the maintained temperature differential—may be elicited at

lower body temperatures. The relative constancy of the temperature differential (body-ambient) at any ambient temperature that is seen initially at 60 days, and its gradual increase at lower ambient values in older animals indicates the presence of a regulatory mechanism which is becoming increasingly responsive.

3. A series of derived relations are pre-

sented to provide suitable indexes for the rate of development which may be summarized as proceeding at a rate of 2.5°/day (temperature at which a given degree of regulation is achieved) or 20 per cent/day (maximum temperature differential possible without a reduction in body temperature) during the maturation period (65–90 days), and at 5 per cent/day thereafter.

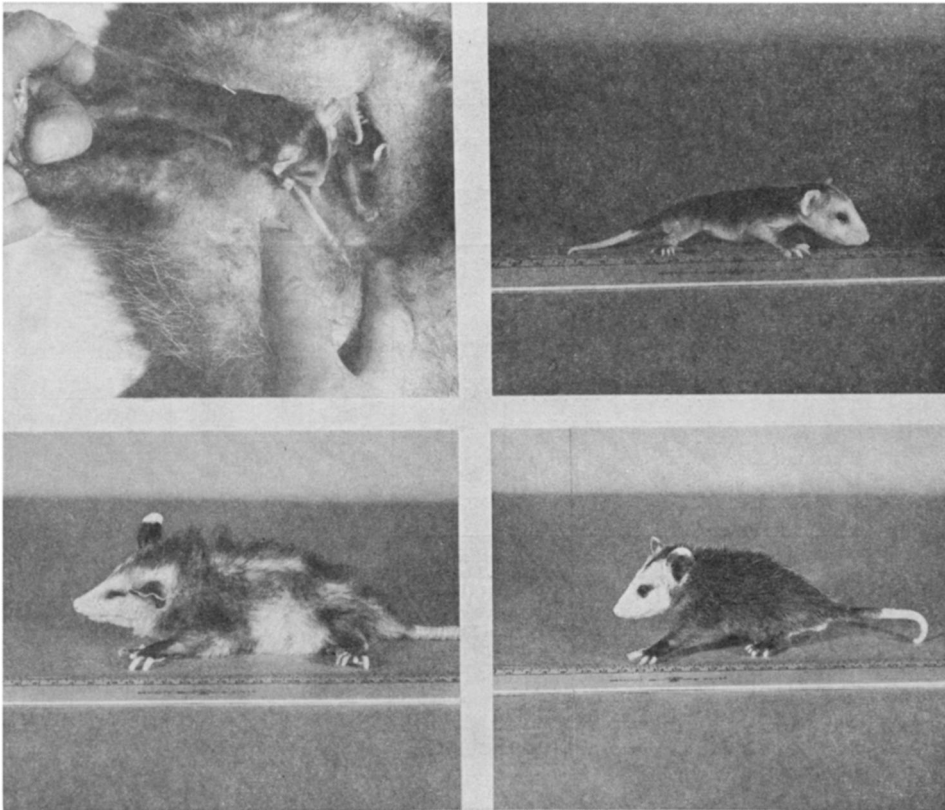


FIG. 11.—Proceeding clockwise: 67-day-old animals in the pouch; 67-day-old animal; 84-day-old animal; 108-day-old animal.

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