THE EFFECTS ON RATS OF CHRONIC EXPOSURE TO 34°C

II. GROWTH

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Summary

The growth rate of female rats kept at 21, 27, and 34°C was measured from weaning to 20 weeks of age and during pregnancy and lactation. Weights of their pups were measured at birth, during the lactation period, and at weaning. Carcass analyses were carried out for lactating females at the end of lactation and for non-pregnant controls.

At 20 weeks of age the weights of virgin rats kept at 27°C were significantly higher than those of rats kept at 21 or 34°C. This was not due to changes in the contribution made to body weight by water or fat.

During pregnancy the gain in weight of rats kept at 34°C was not as great as that of rats kept at 21 and 27°C. This was due, in part, to a reduction in the gain in weight of the mother herself and in part to a reduction in the pup weight, especially when the litter was large.

The increases in weight of lactating females kept at 21 and 27°C were greater than those of non-lactating controls kept at the same temperatures. Controls at 34°C also increased in weight, but lactating females kept at this temperature decreased in weight. The increase over and above the control level in the lactating animals kept at 21 and 27°C was due to an increase in the lean body weight, lean mammary gland weight, and to an increase in the amount of food held in the gut. These increases more than compensated for the small fat losses. Though the lactating animals kept at 34°C showed an increase in mammary tissue and in the amount of food held in the gut, this did not compensate for the marked depletion in the fat stores of these animals. Their weights were therefore below those of the virgin controls kept at the same temperature.

The birth weight of pups born to mothers gestating at 34°C, but littering at room temperature, was significantly lower than that of pups born to mothers gestating at 21 and 27°C. Adjustment for litter size and gestation length increased the differences between the high-temperature and moderate-temperature groups. Growth rate of pups was depressed when mothers and litters were returned to 34°C when pups were 4 days old. Pups born to mothers gestating at 21 and 27°C did not show this decline in growth rate. All three groups showed a decline in the rate of weight increase during the second and third week of lactation. The weaning weight of pups reared at 34°C was significantly lower than that of pups reared at 21 and 27°C.

I. Introduction

Growth of weanling animals of a number of species is known to be affected by high environmental temperature: stunting following exposure to heat has been observed in mice (Sundstroem 1922; Ogle 1934), rats (Sundstroem 1930), pullets

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(Allee and Lutherman 1940), and rabbits and cattle (Johnson, Ragsdale, and Cheng 1957). The minimum temperature at which this effect appears varies between species and between strains of a species. The growth of Shorthorn cattle at 80°F (26·7°C) was slower than that of animals at 50°F (10°C) but the reverse was the case for Brahmin cattle (Ragsdale, Cheng, and Johnson 1957). For mice the minimum effective temperature is apparently above 28°C, as Biggers *et al.* (1958) were unable to demonstrate stunting at 28°C. Strain differences have also been demonstrated for this species by Harrison, Moreton, and Weiner (1959) who observed that while some strains of mice grew better when kept at 90°F (32°C) than at 70°F (21°C), the reverse was the case for others. It is also possible that the diet used may affect the response, for Mills (1945) reported that growth rates of mice kept at 90°F (32°C) could be increased to control levels by adding thiamine, choline, and protein supplements to the diet, and Pennycuik (1964) observed that vitamin and liver supplements improved both growth and reproduction in rats reared at 34°C.

Although no measurements appear to have been made on the effects of heat on the weight changes occurring in the mother during pregnancy and lactation, some measurements have been made on the birth weights and weaning weights of her offspring. Yeates (1956) showed that lambs born to ewes exposed to high day temperatures throughout pregnancy were lighter than those of control animals, and King (1935) showed that birth weights of Norway rats were depressed in the summer. The results of Ragsdale, Cheng, and Johnson (1957) for Shorthorn calves suggest that heat may also affect growth of the young during lactation. Calves which had been hand-fed from 1 month of age onwards grew more slowly at 80°F (26·7°C) than at 50°F (10°C).

This depression in body weight could be due to a reduction in the amounts of nitrogen, fat, or water stored, or to changes in the contribution made by various organs to the body weight, or to combinations of these factors.

Results of nitrogen-balance studies are contradictory. Caspari and Schilling (1920, quoted by Mitchell and Edman 1951) and Mitchell, Hamilton, and Haines (1949) found no differences in the nitrogen balances of men in the tropics and under temperate conditions. However, these studies were made over relatively short periods for adult subjects and small differences may not have been apparent. Conn (1949) found a negative nitrogen balance for men during the first 2–4 weeks of exposure to high temperatures, but balance was restored at the end of this time. This negative balance during the period of acclimatization may account for the assertion of Graham *et al.* (1959) that protein metabolism is increased at high environmental temperatures, as their sheep were acclimatized for periods of only 1 week. Longer exposures were used by Mefferd, Hale, and Martens (1958) in their experiments with rats. Calculation of balances from the data given by these authors suggest that while food intake (and therefore protein intake, since stock diets were used for experimental and control animals) was reduced to approximately 77% of the intake of controls, urinary nitrogen excretion was only reduced to 94%. Whether these relatively high levels of nitrogen excretion were due to depressed synthesis or to preferential utilization of protein for energy production is not clear.

Howard (personal communication, 1961) observed that the fat content of the bodies of rats kept at 34°C lay at the lower end of the range of that for rats at 27°C. The water content of the bodies of these animals, on the other hand, was slightly higher than that for those at more moderate temperatures.

There is evidence that reduced body weight is due in part to a reduction in the contribution made to the body weight by certain organs. Sundstroem (1930) observed that in rats reared at high temperatures liver, spleen, and kidney weights, when expressed as percentages of body weight, fell with increasing temperature, and Howard (personal communication, 1961), working with male rats kept at 27 and 34°C, found that the reduction in the weight of the skin and viscera of the animals at the higher temperature accounted for half the difference in the liveweights between the two groups of animals.

The present experiments were designed to investigate the effects of exposure to 21, 27, and 34°C on growth of female rats from weaning to the age of 20 weeks and on growth and body composition of pregnant and lactating females and non-pregnant controls. Birth weight, growth during lactation, and weaning weight were recorded for the offspring of these females.

II. Materials and Methods

(*a*) *Temperature Control*

The incubators used were the same as those described in Part I of this series (Pennycuik 1964).

(*b*) *Diets*

For the most part, the diet used was the wheat–liver–casein diet described in Part I (Pennycuik 1964). However, for certain calculations results for animals on supplemented stock diets were also included. Analysis of these results showed that they were not significantly different from those of animals on the wheat–liver–casein diet.

(*c*) *Procedures*

The animals used were females born to mothers reared at room temperature. At weaning these were divided into three groups and placed in cages kept at the three experimental temperatures. Each animal was weighed at this time and at weekly intervals until she was 20 weeks of age. At this stage some animals in each group were mated, and those which were not were used later for carcass analyses. Pregnant animals were weighed on the day of service, at intervals throughout pregnancy, and on the day of parturition. Animals were allowed to litter at room temperature and to complete the first 4 days of lactation at the same temperature. Weights of lactating animals were recorded daily from parturition to 21 days lactation, when mothers were separated from their litters. Some females from each group were killed for carcass analysis at this point, and weight changes for others being recorded for another 5 or 6 days.

New litters were looked for at least once a day and pups were weighed to 0·01 g at this time. In a few cases these animals could have been up to 23 hr old

before they were found. It is unlikely that this greatly affected the results, for Murray (1941) found little change in the weights of rat pups over the first 24 hr of extra-uterine life.

In order to make results comparable from one group to another, it was necessary to correct for litter size and length of gestation since both these parameters were affected by heat exposure. (The influence of maternal weight at service on birth weight was so small that it was decided to ignore this factor.)

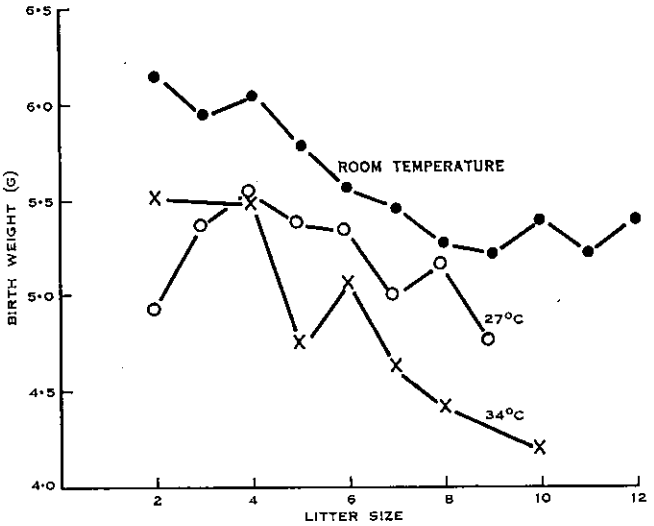

Fig. 1.—Relationship between birth weight and litter size for rats gestating at room temperature and at 27 and 34°C. The numbers in each litter class at each temperature are shown in the tabulation below:

	Litter Size:										
	2	3	4	5	6	7	8	9	10	11	12
	No. of Litters										
Room temp.	1	2	3	2	8	8	10	11	4	2	1
27°C	1	1	3	2	1	5	4	7			
34°C	1		2	4	9	3	3	1			

The correction for each additional pup in the litter was obtained from the graphs relating birth weight to litter size for litters born to stock animals at room temperature and to animals kept at 27 and 34°C which gestated for 22 days (Fig. 1). These corrections gave falls of approximately 0·12 g for each additional pup in the litter for animals at room temperature and 0·20 g for each additional pup for animals at 34°C. These results are comparable with those of Murray (1941) who found a depression of 0·1 g in birth weight for each additional pup in the litter. Increased litter size exerted a more marked effect on birth weights at 34°C than

at lower temperatures. The value for the animals at room temperature was used as the correction factor for animals kept at 21 and 27°C.

In order to calculate the influence of length of gestation on birth weight, results for birth weights were grouped according to litter size; results for mothers gestating for 22 days were averaged and birth weights of pups from longer or shorter gestation

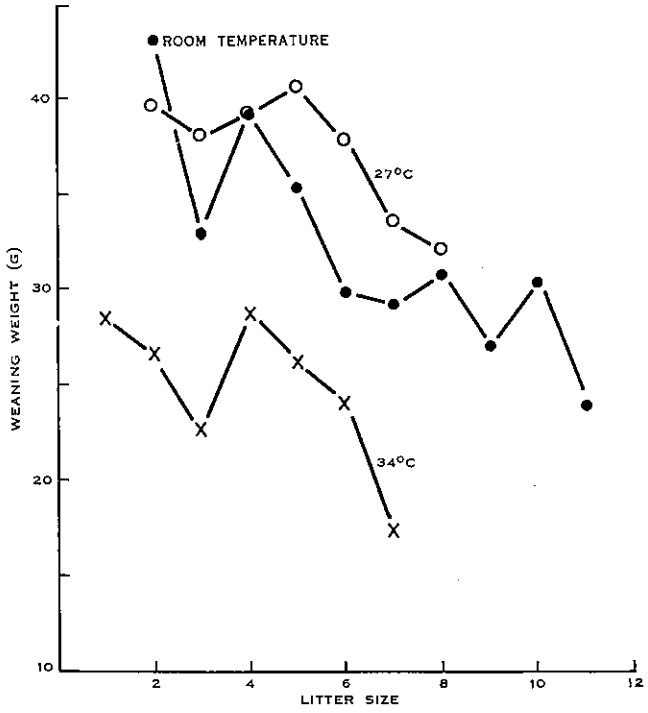

Fig. 2.—Relationship between weaning weight and litter size for rats lactating at room temperature and at 27 and 34°C. The numbers in each litter class at each temperature are shown in the tabulation below:

	Litter Size:										
	1	2	3	4	5	6	7	8	9	10	11
	No. of Litters										
Room temp.		2	5	9	11	11	7	12	8	3	2
27°C		3	3	3	3	3	3	8			
34°C	2	3	2	7	2	1	1				

periods were subtracted from this value. Allowance was made for the number of additional days gestation, then all differences were averaged. These calculations resulted in a correction factor of 0·25 g increase in pup weight for each day for which the pregnancy was prolonged. Although Murray (1941) did not measure the influence of length of gestation on birth weight, his curve for the growth of pups throughout the

pre- and postnatal periods suggests that the gains over the 22–24 days following service are of the same order of magnitude.

Throughout the lactation period, litters were weighed as a group but at weaning (21 days) pups were weighed individually. The influence of litter size on weaning weight was estimated from the graph relating these two parameters (Fig. 2). An average value of 1·25 g for each additional pup in the litter was used as a correction factor for all groups.

Carcass analyses were made of females killed at the time their litters were weaned (21 days) and of virgin animals killed when they had reached the same age. Since the oestrous cycle affects the water content of the carcass, only animals in dioestrus were used. The animals were killed by ether inhalation and, in the case of the lactating animals, this occurred within 10 min after separation from their litters. It was thought that the milk content of the mammary glands would thus be

TABLE 1

WEIGHTS OF RATS KEPT AT 21, 27, AND 34°C AT 20 WEEKS OF AGE, AND OF THEIR PUPS AT BIRTH AND AT WEANING

Values in parentheses indicate the number of animals in each group

	Weight (g)±S.E.		
	21°C	27°C	34°C
20 weeks	152±3·65 (16)	164±3·65 (16)	146±3·65 (16)
Birth	5·2±0·09 (47)	5·1±0·04 (284)	4·9±0·04 (180)
Birth (corrected)*	4·9	5·0	4·7
Weaning (21 days)	34±0·91 (35)	35±0·44 (145)	26±0·68 (62)
Weaning (corrected)†	33·5	34·5	22·5

* Adjusted to a gestation length of 22 days and a litter size of six.

† Adjusted to a litter size of six.

approximately the same in all rats. The weight of the body at this time, weighed to 0·03 g, was taken as the "liveweight". Hair was then removed with clippers and the weight of the hair recorded; the skin was stripped back and the mammary glands dissected out and weighed; the alimentary tract was removed and stripped of food, the gut contents weighed, and the alimentary tract returned to the body. Body and gut contents were dried in an oven at 90°C for a minimum of 4 days, which was the time required for the attainment of constant weight. These were then reweighed. The bodies were than crushed and fat extracted in a Soxhlet extractor with isopropyl ether for 8 hr. The solvent was distilled off at the end of that time and the extracted fat was estimated. Lean body weight was calculated by subtracting the weight of hair, gut contents, and fat in the carcass from the liveweight. Lean liveweight was calculated by subtracting the weight of fat in the body from the liveweight (i.e. gut contents and hair were included in this value). Body water included both carcass water and gut water.

III. Results

(a) *Weights of Virgin, Pregnant, and Lactating Rats*

The weights of the experimental animals at 20 weeks of age are shown in Table 1. Results for those kept at 21 and 34°C were both significantly below those for animals kept at 27°C. The optimum temperature for the growth of rats given this particular diet appears to be close to 27°C.

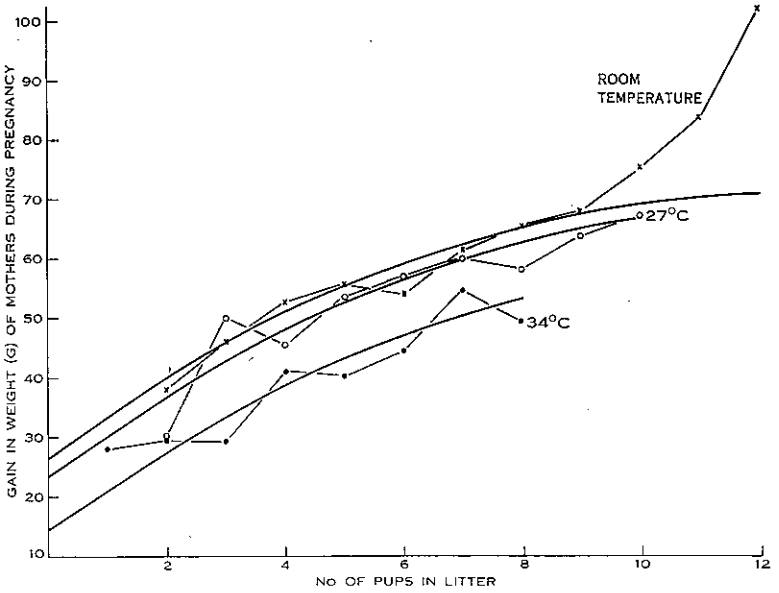

Fig. 3.—Relationship between maternal weight gain during gestation and litter size for rats gestating at room temperature and at 27 and 34°C. The numbers in each litter class at each temperature are shown in the tabulation below:

	Litter Size:											
	1	2	3	4	5	6	7	8	9	10	11	12
	No. of Litters:											
Room temp.		2	1	6	4	14	9	12	18	15	12	1
27°C		1	2	4	3	5	4	7	5	2		
34°C	1	4	7	7	10	21	12	9				

Average values for the weight gains during pregnancy were plotted against litter size (Fig. 3). The weight gain of the mother is composed of two elements: the weight of the foetuses carried and the increase in the body weight of the mother herself. Since birth weight is inversely related to litter size (Fig. 2), one would expect the relationship between weight gain of the mother and litter size to be a curve. This appears to be the case. The intercepts of these curves represent the weight gained by the mother herself during the gestation period. This increase

in maternal weight is probably due to water retention, nitrogen retention, and to an increase in the amount of food held in the gut (Dewar 1953). The fact that the value for the intercept for the animals kept at 34°C is smaller than that for animals kept at 27°C or at room temperature suggests that females at 34°C store one or more of these elements less efficiently than their sisters at more moderate temperatures.

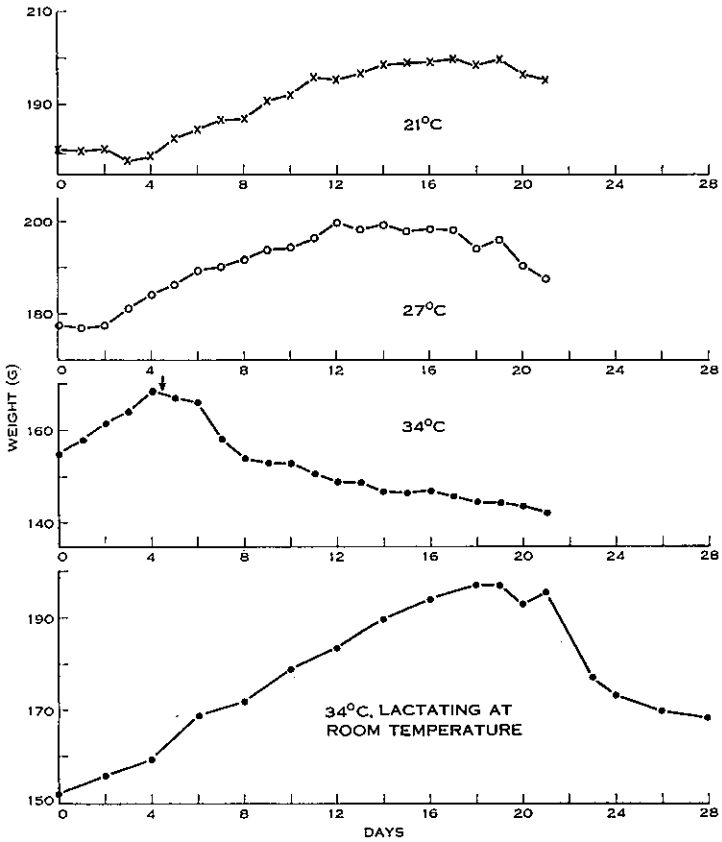

Fig. 4.—Maternal weight changes during lactation each for five rats kept at 21 and 27°C and for four rats kept at 34°C during gestation but which commenced lactation at room temperature and completed it at 34°C (these were returned to 34°C at the point indicated by the arrow). Weight changes for a second group of four rats kept at 34°C but which were allowed to lactate at room temperature are also shown.

Weight changes during lactation are illustrated in Figure 4. Similar curves were obtained for animals on other diets. Animals kept at 21 and 27°C showed an increase in weight over this period. Those reared at 34°C also showed an increase while they remained at room temperature but their weights fell steadily to a level below that at parturition when they were returned to 34°C. However, if they were allowed to complete lactation at room temperature, these animals at 34°C showed a weight increase similar to that of animals kept at 21 and 27°C.

TABLE 2

CONTRIBUTION MADE BY LEAN BODY WEIGHT, LEAN MAMMARY GLAND WEIGHT, FAT, GUT CONTENTS, AND HAIR TO THE LIVEWEIGHT OF VIRGIN AND LACTATING RATS REARED AT 21, 27, AND 34°C

Temp. (°C)	No. of Rats	Size of Litter at 21 Days	Liveweight (g) ±S.E.	Composition (±S.E.) as % of Liveweight					Water as % of Lean Liveweight (±S.E.)
				Lean Body Weight*	Lean Mammary Gland Weight	Fat	Gut Contents	Hair	
21	6 (virgin)	—	169±5·78	79·9±0·81	0·71±0·06	14·5±0·38	2·96±0·30	1·91±0·05	70·6±0·14
	5 (lact.)	5·4	194±6·34	79·5±0·89	3·74±0·58	10·7±1·30	4·58±0·33	1·50±0·06	72·3±0·34
27	4 (virgin)	—	190±7·09	79·1±0·99	0·77±0·05	15·5±1·48	2·94±0·37	1·76±0·06	71·3±0·10
	6 (lact.)	5·8	194±5·78	81·2±0·81	3·56±0·22	8·2±0·90	5·69±0·30	1·40±0·05	72·2±0·22
34	6 (virgin)	—	158±5·78	82·2±0·81	0·78±0·03	11·7±0·42	3·63±0·30	1·71±0·05	71·5±0·16
	3 (lact.)	2·7	144 (135—160·5)†	85·2 (84·1—86·3)†	2·99 (2·54—3·42)†	5·7 (4·6—7·2)†	4·49 (3·66—4·98)†	1·67 (1·43—1·91)†	72·0 (71·4—72·5)†

* This represents the lean body weight minus the lean mammary gland weight.

† Ranges.

(*b*) *Analysis of Weight Change*

The contributions made by lean body weight, lean mammary gland weight, fat, gut contents, hair, and water to the liveweights of virgin and lactating animals at the three environmental temperatures are shown in Table 2. Analysis of animals on other diets gave very similar results. Values for virgin animals show that the compositions of the bodies of animals kept at 21 and 27°C were essentially the same. Animals kept at 34°C, on the other hand, contained less fat. This may have contributed to their lower body weight.

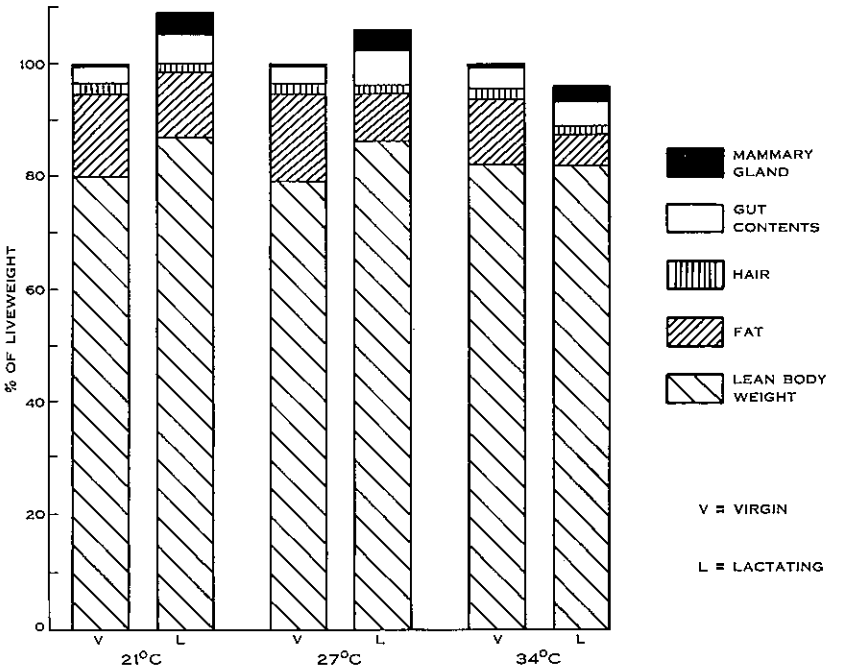

Fig. 5.—Body composition of virgin and lactating rats. Weights of the virgin controls have been taken as 100%, and weights of animals which were pregnant have been expressed as a percentage above or below this value. This percentage was calculated from the difference between the weight gain during pregnancy and lactation of the experimental animals and the weight gain of the virgin controls over the same period. Lactating animals were killed when pups were weaned (21 days), controls were killed when their ages approximated those of their lactating sisters. The numbers in each group are shown in Table 2.

Results for lactating animals, also, indicate that the compositions of the bodies of animals kept at 21 and 27°C were essentially the same. Animals kept at 34°C, on the other hand, contained less fat, smaller amounts of food in the gut, and less mammary tissue. The small contribution made by gut content to the liveweight of all these groups was due to the low volume of the diet.

Results for the same six groups of rats are illustrated graphically in Figure 5. In order to draw up this figure, the weights of the virgin animals at each temperature have been taken as 100%, and the weights of the lactating animals have been

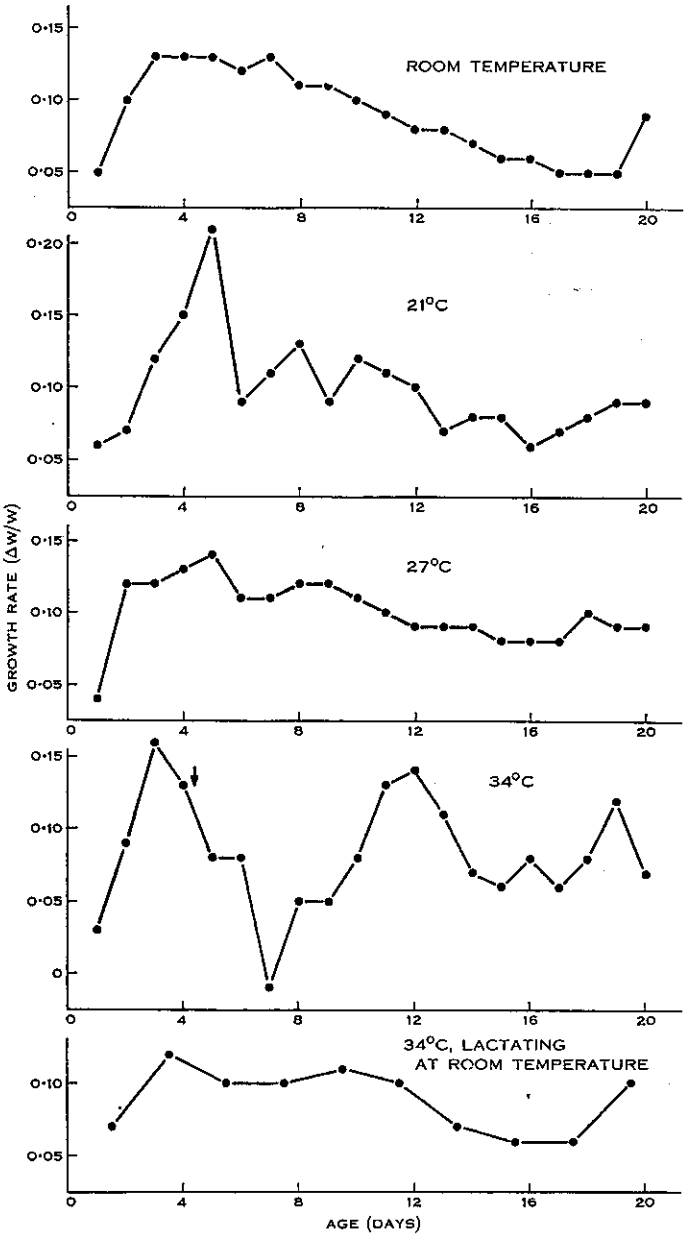

Fig. 6.—Weight changes ($\Delta W/W$) of pups reared during the first 21 days of extra-uterine life at room temperature, 21, 27, and 34°C. (W = weight at time, t, and ΔW the weight change between time t and t_1). The numbers in the groups were as follows:—room temperature, 32 litters, 190 pups; 21°C, 5 litters, 27 pups; 27°C, 5 litters, 36 pups; 34°C, 4 litters, 13 pups; mothers reared at 34°C, litters reared at room temperature, 6 litters, 30 pups.

represented as percentages above or below these values. These percentages were calculated by subtracting the weight gain of controls over a 6-week period from the weight gain of the experimental animals during pregnancy and lactation (6 weeks).

From this figure it is apparent that the weight gains during pregnancy and lactation at 21 and 27°C were due to increases in lean body weight, lean mammary gland weight, and the amount of food held in the gut. These increases more than compensated for fat losses. In animals kept at 34°C the increase in mammary tissue and gut content did not compensate for fat losses and there was no increase in lean body weight. The weights of these animals were therefore below control levels.

At no point can changes in the water content of the body be used to explain differences in body weight, although water as a percentage of lean liveweight (Table 2) was rather higher in the lactating animals than in controls. This was due in part to the presence of more mammary tissue in the latter group. The variability of the results was due to variation in gut water which ranged from 66 to 82% of the gut content.

(c) *Birth and Weaning Weights*

Birth weights of pups born to mothers gestating at 21, 27, and 34°C are shown in Table 1. Even without correction for litter size and gestation length the difference between the group kept at 27°C and the group kept at 34°C is significant.

The weight changes of pups during lactation, $\Delta W/W$, where W = the weight at time t, and ΔW the weight change between time t and time t_1, are illustrated in Figure 6. For the rats kept at room temperature, 21, and 27°C there was a gradual decline in growth rate from the end of the first week onwards. The curve for rats kept at 34°C, on the other hand, showed wide fluctuations; there was a marked fall when mothers and litters were returned to 34°C at 4 days after parturition, a recovery phase during which the rats again adapted to the higher temperature, then a second decline in growth rate comparable with that for pups at 21 and 27°C.

This depression of the growth rate of pups during lactation led to a depression of the weaning weight (Table 1). The difference between the weights of rats kept at 27°C and those of rats kept at 34°C was highly significant even without adjustments for litter size.

IV. Discussion

It is clear that exposure to high environmental temperature depresses growth, not only in the post-weaning period, but at all phases investigated. The cause of this depression is probably not the same in all cases.

Growth during the prenatal and early postnatal period is said to be inherent in the embryonic tissue, for maternal and foetal hormones have very little effect during this phase (Jost 1954). So far no mechanism has been suggested to explain how high environmental temperature depresses growth during this period.

Growth of the pups during lactation will depend upon the direct effect of heat on the young and upon its effects on the mother and her milk supply. That heat may exert a direct effect on the young animal is shown in the experiments

of Ragsdale, Cheng, and Johnson (1957) on calves. Brahmin, Shorthorn, and Santa Gertrudis animals were kept at 50°F (10°C) and 80°F (26·7°C) and were hand-fed from 1 month of age onwards. In the case of the Shorthorn calves, those kept at the higher temperature grew more slowly than those at 10°C. The present experiments were not designed to separate the effects of heat on the young from those on the mother, but it is of interest that the greatest reduction in growth rate of the pups occurred when mother and litter were returned to 34°C. This coincided with a period of depressed food intake of the mothers; thus depressed lactation appears to be a likely cause of slower growth.

The second more gradual decline in growth rate which occurred during the second and third week of lactation may also be due in part to a reduction in milk supply, for it has been postulated that failing milk supply and the changeover from a milk diet to a solid diet are responsible for the decline in growth rate over this same period in pups reared at lower temperatures (Parkes 1926; McDowell, Gates, and McDowell 1930; Murray 1941).

Inanition does not explain reduced growth during the post-weaning period or during pregnancy and lactation, since food supplies were unrestricted and, in spite of differences in caloric intake, protein, salt, and vitamin intakes were the same in all three groups. Moreover, the animals showed none of the physical changes usually associated with semi-starvation (Asdell and Crowell 1935). In the post-weaning animal the differences in weight appear to be due largely to an overall reduction in the body components though a reduction in the contribution made by skin and viscera to body weight probably accounts for part of the difference (Howard, personal communication, 1961).

In lactating rats kept at 34°C the reduction in growth was due, in part, to slowed growth of the lean body mass, for there was a difference in this component of approximately 8% between the group at 34°C and the groups at lower temperatures. In both growing and lactating rats, their smaller size at 34°C implies an impaired retention of nitrogen. This could be due to impaired absorption, an increase in the obligatory catabolism of protein, or to a depression of protein synthesis. Impaired absorption seems an unlikely explanation in these experiments for the protein intake was very high (3 g/rat/day) when compared with that for animals on stock diets. Moreover, protein absorption is known to depend on the level of protein intake over a wide range of environmental temperatures (Graham *et al.* 1959). Increased protein catabolism at elevated temperatures (Graham *et al.* 1959) probably occurs mainly during the acclimatization period, for Conn (1949) found that nitrogen balance was restored in men after they had been allowed to acclimatize to high temperatures for 2–4 weeks. Depression of protein synthesis, therefore, seems to be the most likely explanation.

This failure to utilize metabolites available in food could be due to changes in nutritional requirements, hormonal changes, or enzymatic changes at high environmental temperatures.

Nutritional requirements are known to be affected by high environmental temperatures (Mitchell and Edman 1951). However, several different diets have been tried in this Laboratory and though the intakes of both vitamins and proteins were

varied over a wide range it was not possible to return the growth rate of animals kept at 34°C to the same level as that of animals kept at 27°C (Pennycuik 1964). These results are at variance with those of Mills (1945) for mice.

The level of thyroxine is known to be depressed in animals at high temperatures (Dempsey and Astwood 1943; Hurst and Turner 1947), and there is a suggestion that 17-ketogenic steroid levels are also reduced (Robinson and Morris 1960). The effects of heat on the production of other hormones known to affect growth have not been investigated though indirect evidence suggests that the output of these also is depressed; for example, Sundstroem (1930) observed a reduction in the size of the testis, suggesting reduced androgen production; and Bonsma (quoted by Hammond 1949) suggested that the lowered fertility of European cattle under tropical conditions might be due to inhibition of anterior pituitary development, suggesting an interference with growth hormone production. All these hormones are known to influence growth (Gaunt 1954), but thyroxine and androgen are thought to influence body proportions, and altered proportions is not one of the characteristics of animals exposed to high environmental temperatures. High rather than low corticoid levels are thought to inhibit growth and, on the evidence of Robinson and Morris (1960), the excretion of 17-ketogenic steroids, at least, is reduced in the heated animal. It is regrettable that growth hormone measurements have not been made in animals exposed to high environmental temperatures for they share several characteristics in common with hypophysectomized animals. Both show a reduction in the relative weights of liver, spleen, and kidneys (Smith 1930; Sundstroem 1930) and both show a more marked reduction in weight than in length (Clayton and Worden 1960; and present experiments).

Potter (1958) pointed out that while the genetic constitution of the animal limits the enzyme systems possible, environment determines which ones will actually develop. Changed hormonal levels are known to affect tissue enzymes (e.g. Wilmer 1960*a*, 1960*b*) and, whether mediated by this or by some other means, tissue enzymes are known to vary in animals reared at high environmental temperatures (Knox, Auerbach, and Lin 1958; Mefferd, Nyman, and Webster 1958; Kanungo and Prosser 1959). Since many of these enzymes are directly or indirectly concerned in tissue synthesis, variations in their concentrations may ultimately be responsible for variation in the growth rate of animals exposed to heat.

It is probable that differences between animals reared at moderate and at high temperatures are hormonal and enzymatic in origin, and that changes in the levels of these two components account for differences in abilities to retain nitrogen and for differences in relative organ weights.

V. References

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