THE EFFECTS ON RATS OF CHRONIC EXPOSURE TO 34°C

III. APPETITE AND THE EFFICIENCY OF FOOD CONVERSION

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Summary

The food intake of growing rats declined progressively with rising temperature. The food intakes of lactating rats kept at 21 and 27°C increased throughout lactation. The intake of gestating rats kept at 34°C decreased when they were returned to 34°C after being allowed to litter at room temperature. Throughout lactation, the intakes of animals kept at 21 and 27°C were greater than those of rats kept at 34°C.

Among growing rats of all age groups, food was used more efficiently by those kept at 34°C than by those reared at lower temperatures. In suckling animals, also, efficiency appeared to be greater at 34°C. However, when the calorie cost of maternal fat losses was included in the calculation this difference was eliminated.

Fat stores were smaller in growing rats reared at 34°C than in those reared at 21 or 27°C. Fat stores were depleted in all lactating animals but this depletion was greatest in the rats kept at 34°C.

I. Introduction

In the rat, food intake has been found to fall proportionally as environmental temperature is raised (Brobeck 1948; Kennedy 1952–53). With the exception of acute exposures to high temperature, body weight is maintained (though growth may be slowed) despite this lowered food intake. The fall in food intake, therefore, must be related to a fall in energy expenditure or to increased absorption, increased metabolic efficiency, reduced synthesis, reduced excretory losses, or to a combination of these factors.

A decrease of energy expenditure appears to be the most important factor in reducing the food intake as environmental temperature rises. Below the zone of thermal neutrality, the cost of maintaining body temperature falls as environmental temperature rises. Graham *et al.* (1959) observed a fall in the metabolism of the sheep of the order of 115 kcal/24 hr/degC rise in environmental temperature. Above the zone of thermal neutrality the cost of maintaining body temperature, under basal conditions, rises (Brody 1945). However, at temperatures above this zone, animals become less active (Howard *et al.* 1959) and total energy expenditure probably falls for several degrees above the upper end of this zone.

There is evidence that increased absorption and reduced excretory loss also contribute to the fall in energy expenditure (Graham *et al.* 1959). Reduced synthesis may also be of some importance, for growth may certainly be demonstrated in animals kept at high environmental temperature (Pennycuik 1964*b*).

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Evidence for or against increased metabolic efficiency is still wanting, as most calculations of efficiency involve *total* food intake but *net* synthesis; that is, a reduction in the amount of energy expended in body processes other than growth will lead to an apparent increase in the efficiency of food utilization. So far no attempt has been made to eliminate, or to compensate for, these differences in expenditure in animals at high temperatures. Kennedy (1957) pointed out that young rats employ the major part of the food available to them for growth, and conversion rates for these animals may possibly provide a partial answer to this question.

Where no compensations have been made for differences in energy expenditure, results for efficiency of animals kept at high environmental temperatures are contradictory. This is probably due to differences in the amounts of energy expended on cooling and on activity by the animals in the different experiments. Using mice acclimatized to 90°F (32·2°C) and to 70–75°F (21·1–23·9°C) Mills (1945) found that efficiency of food conversion was better at the higher temperature. Heitman and Hughes (1949), using pigs exposed to various experimental temperatures for test periods of 7 days, found maximum efficiency of food utilization at temperatures which permitted maximum gains: for example, pigs weighing 100–150 lb (45·4–68·2 kg) showed an optimum at 70°F (21·1°C), while pigs weighing 350 lb (159·1 kg) showed an optimum at 61°F (16·1°C). Johnson (quoted by Warwick 1958) found that when pigs weighing 150 lb (68·2 kg) were acclimatized to temperatures of 50°F (10°C) and 90°F (32·2°C) for 32 days efficiency was greater at the lower temperature, but that when the animals were acclimatized to the two temperatures from weaning to 200 lb (90·9 kg) there was no significant difference in the efficiency of conversion.

Since body weight is maintained satisfactorily at high environmental temperatures, it is clear that the centres controlling food intake function normally in animals allowed to adjust their activities at these temperatures. That those centres are also able to adjust to increased muscular activity under these conditions has been shown by Consolazio *et al.* (1960) who observed that troops carrying out routine duties in the Arizona desert (mean daily average temperature range 33·9–36·1°C) were able to increase their food intake to 4000–4500 calories per day, a quantity equal to that eaten by troops doing hard physical work under more temperate conditions. Whether or not centres controlling food intake are able to adjust to enforced increase in synthetic activity at these temperatures does not appear to have been investigated.

In the course of measuring growth rate on different diets (Pennycuik 1964*b*), it was necessary to estimate the food intakes of growing and lactating rats kept at 21, 27, and 34°C. These data are presented, together with estimates of the efficiency of conversion of foodstuffs in both suckling and weanling animals. In order to assess the value of the conversion rates for suckling animals, it was necessary to measure fat reserves in lactating and control females. These values also have been included.

II. MATERIALS AND METHODS

The animals and the incubators used were the same as those described in Part I of this series (Pennycuik 1964*a*). The diet used was one based on wheat–liver–casein described in the same paper.

Measurement of food intake for growing animals was made for females born to mothers reared at room temperature and divided randomly at weaning into three treatment groups. Within each treatment group 8–13 rats were housed in a cage. Food was given in a container with a wire grid in front to prevent spillage. Food intake was measured by weighing this container each day before and after filling.
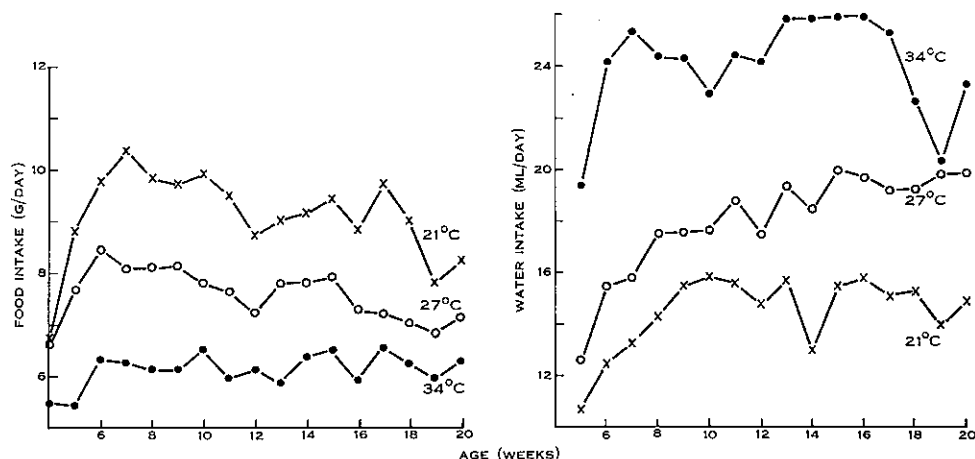

Fig. 1.—Intake of food and water by rats kept at 21, 27, and 34°C from 4 to 20 weeks of age.

Results for each week were averaged (Fig. 1). Food efficiency was calculated by dividing the weight of the food consumed by the weight gained by the rat over the same period (Bradfield and Maynard 1958). Caloric intake was calculated by multiplying the food intake by the caloric values of the diets used; these were: 21°C, 3·6 kcal/g; 27°C, 3·5 kcal/g; 34°C, 3·4 kcal/g. The efficiency of conversion of food calories to rat tissue was calculated by converting the food intakes to caloric intakes and dividing by the weight gained.
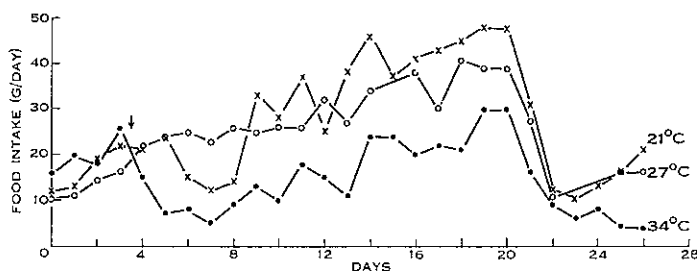

Fig. 2.—Food intake of rats lactating at 21°C (1 rat, litter of 8), 27°C (1 rat, litter of 5), and 34°C (1 rat, litter of 5); this animal littered at room temperature and was returned to 34°C 4 days later (arrow).

Throughout lactation, individual cages housing one mother and her litter were used. Food intakes for mothers and litters were measured in a manner similar to that for growing rats. Daily intakes were used in plotting representative curves at the three temperatures used (Fig. 2). Costs of maintenance of each pup over 21 days were

calculated by subtracting the cost of maintenance of the non-pregnant female over 21 days from the amount of food eaten by the lactating animal and her litter over the same period and dividing by the number of pups in the litter. Food efficiency was calculated by dividing this value by the weight gained by the pups during the lactation period. The efficiency of conversion of food calories to rat tissue was calculated by converting the cost of maintenance of each pup to calories and dividing by the weight gained.

The contribution made by fat to the total body weights (i.e. liveweight minus the weight of hair and gut contents) of virgin and lactating rats was estimated by extracting the fat with isopropyl ether in a Soxhlet extractor. Details of the procedure have been described in Part II (Pennycuik 1964b).

TABLE 1

FOOD AND CALORIC INTAKES OF SIXTEEN 20-WEEK-OLD RATS (WT. 140–170 G) REARED AT 21, 27, AND 34°C AND EFFICIENCIES OF CONVERSION OF FOOD AND FOOD CALORIES TO RAT TISSUE BY THESE RATS BETWEEN WEANING AND 20 WEEKS OF AGE

Temp. (°C)	Food Intake (g/rat/day)	Calorie Intake (kcal/rat/day)	Conversion Ratios at:							
			4–7 Weeks		8–11 Weeks		12–15 Weeks		16–19 Weeks	
			Food*	Calories†	Food	Calories	Food	Calories	Food	Calories
21	9·0	32·5	3·73	11·4	12·50	45·0	16·61	59·8	76·41	275·1
27	7·3	25·3	3·39	11·9	8·21	28·7	11·73	41·1	24·15	84·5
34	6·3	21·5	3·24	11·0	5·94	20·2	10·46	35·6	20·35	69·2

* Ratio of food consumed to weight gained.   † Ratio of caloric intake to weight gained.

III. RESULTS

(a) Growing Rats

Intakes of food and water for rats kept at 21, 27, and 34°C from weaning to 20 weeks of age are illustrated in Figure 1. These results confirm earlier observations that food intake falls as environmental temperature rises, while water intake rises with rising temperature. The form of the food intake curve differed in the three groups of animals studied. For those at 21 and 27°C, the intake fell after an initial steep rise between the ages of 4 and 6 weeks, but those at 34°C showed a very constant intake from 6 weeks of age onwards. Murray (1941) observed a fall similar to that of the groups kept at 21 and 27°C in his animals, which were kept at room temperature.

(b) 20-week-old Rats

Food and caloric intakes at 20 weeks of age are presented in Table 1. These agreed closely with those obtained for other diets (Pennycuik, unpublished data). The efficiency of food utilization is shown in the same table. For all age groups the conversion rates, considered in terms of food or calories, were slightly greater for the

animals kept at 34°C than for those at lower temperatures. For the 4–8-week period, the difference in efficiency was small, but the slowing of the growth rate with advancing age coupled with the continued high food intake at the lower temperatures led to greater differences in the older age groups. This was particularly marked for animals kept at 21°C during the 16–20-week period.

Considered in terms of protein, conversion at 34°C was not as efficient as that at 21 or 27°C since the diets were arranged so that the intake was the same for all animals at the three different temperatures used, viz. approximately 3·0 g/rat/day. Since the weight gain over the same period was considerably less than this, it is clear that in all cases the excess protein was either being used for purposes other than growth or was not absorbed.

TABLE 2

FOOD AND CALORIES, FROM BOTH FOOD AND MATERNAL STORES, USED TO MAINTAIN EACH PUP FROM BIRTH TO WEANING AT 21 DAYS

Efficiencies of conversion of food and calories to rat tissue over the same period are also given

Temp. (°C)	No. of Litters	No. of Pups	Weight Increment (g/pup)	Food Consumed		Conversion Ratios		
				(g/pup)	(kcal/pup)	Food*	Calories†	Food + Fat‡
21	5	27	30	61·6	221	2·05	7·38	8·6
27	5	36	30	60·8	213	2·03	7·10	11·0
34§	4	13	22	46·1	157	2·12	7·23	12·3
34‖	4	13	18	32·8	112	1·80	6·13	11·2

* Ratio of food consumed (g) to weight gained (g).

† Ratio of calories consumed (kcal) to weight gained (g).

‡ Ratio of food (kcal) consumed + storage fat (kcal) used to weight gained (g).

§ Values for 21 days (birth to weaning) lactation and include the initial period of from 4 to 5 days during which mothers and litters were exposed to room temperature.

‖ Values for period from day 8 to day 21 inclusive (i.e. 14 days) when rats were exposed to 34°C only.

(c) Lactating Rats

The food intake of lactating mothers kept at the three experimental temperatures is illustrated in Figure 2. (Only animals for which measurements following weaning were available have been used for this figure. Results for animals killed at weaning showed the same pattern up to this point.) At all temperatures investigated, there was an increase in food intake during lactation (cf. Slonaker 1925; Hitchcock 1927; Murray 1941). At 21 and 27°C this increase was regular, but at 34°C the rise in intake after parturition at room temperature was followed by a marked fall when mother and litter were returned to 34°C, 4 or 5 days after parturition. Peak intakes at 34°C were 10 g below those at 27°C and almost 20 g below those at 21°C. Exposure to room temperature after parturition provided a greater stimulus to appetite in this animal than feeding five pups at 34°C. At all temperatures, there was a sharp drop in maternal intake during the 2 days following weaning. This was partly due to the removal of the pups which started to eat solid food at about 14 days of age, but

probably the mothers ate less also at this period. At the lower temperatures, maternal intake increased again after 2 or 3 days, but at 34°C it continued at a low level.

(d) Energy Conversion in Pups

The costs, in food and calories, of maintaining each pup during the lactation period (21 days) are shown in Table 2. For the groups at 21 and 27°C there was little difference between costs and both of these estimates are of magnitudes comparable with those found by Slonaker (1925) and Murray (1941). Energy consumption by animals kept at 34°C was appreciably lower. On the other hand, conversion efficiencies (for both food and calories) was of approximately equal magnitude in all three groups when the period at room temperature was included for animals kept at 34°C. Only when this period was omitted was there any appreciable difference between this group and the groups at the lower temperatures.

TABLE 3

FAT CONTENT OF THE BODIES OF VIRGIN AND LACTATING RATS

Values expressed as a percentage of body weight [liveweight−(weight of hair+weight of gut contents)]

Temp. (°C)	No. of Rats	Mean No. in Litter	Body Weight (g) ±S.E.	Fat Content (%) ±S.E.
21	6 (virgin)	----	160±5·30	15·3±0·37
	5 (lactating)	5·4	182±5·80	11·4±1·37
27	4 (virgin)	----	180±6·49	16·2±1·52
	6 (lactating)	5·8	179±5·30	8·8±0·98
34	6 (virgin)	----	149±5·30	12·3±0·45
	6 (lactating)	2·7	127±5·30	6·6±0·41

The contribution of fat to body weight is shown in Table 3. Values for animals in all groups at the end of lactation were below those of virgin controls. When the caloric values of these fat losses were added to the caloric cost (in terms of food) for each pup, it was apparent that the energy required for an increase of 1 g in pup weight at 34°C was equal to (or possibly slightly greater than) that at 21 or 27°C (Table 2).

IV. Discussion

Results for growing animals confirm earlier observations that food intake falls as environmental temperature rises. The upper limit of the zone of thermal neutrality for rats acclimatized to 34°C was not determined. However, it is probably close to the acclimatization temperature, for Gelineo (1935) found that the thermoneutral point for animals acclimatized to 35·5–36°C was 34°C. It is therefore not possible from these experiments to draw any conclusions about the pattern of food intake above the thermoneutral point. In spite of this lowered food intake, animals kept at 34°C were able to grow and to store fat at levels comparable with that of their litter mates reared at lower temperatures. Moreover, they showed none of the usual

signs associated with inanition (Asdell and Crowell 1935). It is clear that rats kept at 34°C are able to strike a balance between food intake and energy expenditure, very similar to that reached by animals at lower temperatures.

Although rats in all groups used fat stores during lactation, the effect was greatest in the rats kept at 34°C. Moreover, rats in this group were the only ones to show a decline in body weight and a reduction in protein synthesis over this period (Pennycuik 1964*b*). Human subjects undertaking increased activity under desert conditions consumed more food to meet the demands of work (Consolazio *et al.* 1960) but rats kept at 34°C were apparently unable to increase their food intake sufficiently to compensate for the demands of lactation.

Appetite appears to be controlled by the feeding and satiety centres of the hypothalamus (Brobeck 1955, 1960). These in their turn are thought to be affected by body temperature (Brobeck 1948, 1960), gastric motility (Quigley 1955), arterio-venous differences in levels of glucose (Mayer 1955) and other metabolites (Dowden and Jacobson 1960), levels of fat stores (Bruce and Kennedy 1951; Kennedy 1952–53, 1955) and emotional factors (Mayer 1960). These have been reviewed by Andersson and Larsson (1961). Of the five factors mentioned, only two have been suggested as possible mechanisms by which heat could cause a depression of food intake, viz. increased body temperature (Brobeck 1948) and reduced gastric motility (Mitchell and Edman 1951). Though these may contribute to the reduction of appetite in the heat, it is unlikely that they could explain wholly the reduction in food intake for no rise in body temperature was observed in the animals at 34°C, though their food intake was well below that of animals at lower temperatures (Pennycuik, unpublished data). Gastric motility is known to be influenced by arteriovenous differences in glucose levels (Stunkard and Wolff 1954) which may well have been different in animals at the three different environmental temperatures used in the present study.

Differences in arteriovenous levels of glucose and other metabolites seems to be a much more likely mechanism by which appetite could be controlled at high environmental temperatures. Activity is known to be reduced at 34°C (Howard *et al.* 1959), so too is growth, and there is some evidence that metabolic activity is also affected (Mefferd, Nyman, and Webster 1958). All these factors would tend to raise venous metabolite levels and reduce arteriovenous differences in the concentration of these metabolites.

Fat percentages in the bodies of virgin and lactating animals at the three temperatures used suggest that control of appetite by the level of the fat stores of the body is more complex than was originally postulated by Kennedy (1952). Although rats at all three temperatures lost fat during lactation, this effect was most marked in those kept at 34°C. Either lactation altered the level at which these stores were set or control of appetite by this means was eliminated. High environmental temperature apparently increased the fat mobilization due to lactation. Circulating hormonal levels are known to be altered during lactation (Benson *et al.* 1959) and these in their turn are known to influence the metabolic pathways of fat metabolism and rates of fat storage and mobilization (Barrnett and Ball 1960; Engel and White 1960; Odum 1960). Heat may well influence the magnitude of the fat store through a similar mechanism.

The possibility that heat may also influence the feeding and satiety centres through impulses from skin receptors does not appear to have been investigated, though the only known case in which food intake was increased at high environmental temperatures was in the experiments of Consolazio *et al.* (1960) where the subjects were fed in an air-conditioned dining room.

Though the evidence is limited, results for experiments with suckling animals [where food is used almost exclusively for growth (Kennedy 1957)] lend no support to the suggestion that reduced food intake at high environmental temperatures is due in part to increased metabolic efficiency. When that part of the caloric intake devoted to pup growth was added to the caloric value of the fat removed from maternal stores during lactation, the cost of producing 1 g of pup tissue was almost identical for animals at 27 and 34°C.

On the other hand, in growing animals kept at 34°C, where energy expenditure on activities other than growth was reduced, the efficiency of utilization of food was greater than at 21 or 27°C. These results are in agreement with those of Mills (1945) for mice and are not inconsistent with those of Johnson (quoted by Warwick 1958) for pigs acclimatized to 90°F (32·2°C) from weaning onwards. It would appear then that for temperatures up to 34°C, rats acclimatized to the higher temperatures, showed greater efficiency of food utilization than those acclimatized to lower temperatures. The optimum temperature for growth, on the other hand, appeared to be close to 27°C.

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