Murley, W. R., Allen, R. S. & Jacobson, N. L. (1951). *J. Anim. Sci.* **10**, 1057.
Murley, W. R., Jacobson, N. L. & Allen, R. S. (1952). *J. Dairy Sci.* **35**, 846.
Murley, W. R., Jacobson, N. L., Wing, J. M. & Stoddard, G. E. (1951). *J. Dairy Sci.* **34**, 500.
Pritchard, G. I., Riddell, W. H. & Durrell, W. B. (1954). *J. Dairy Sci.* **37**, 654.
Ragsdale, A. C. (1934). *Bull. Mo. agric. Exp. Sta.* no. 336.
Richardson, C. W., Ronning, M., Berousek, E. R. & Norton, C. L. (1953). *J. Dairy Sci.* **36**, 593.
Roy, J. H. B., Palmer, J., Shillam, K. W. G., Ingram, P. L. & Wood, P. C. (1955). *Brit. J. Nutr.* **9**, 11.
Rusoff, L. L., Alford, J. A. & Hyde, C. E. (1952). *J. Dairy Sci.* **35**, 493.
Rusoff, L. L., Alford, J. A. & Hyde, C. E. (1953). *J. Dairy Sci.* **36**, 45.
Rusoff, L. L. & Davis, A. V. (1951). *J. Dairy Sci.* **34**, 500.
Rusoff, L. L., Davis, A. V. & Alford, J. A. (1951). *J. Nutr.* **45**, 289.
Rusoff, L. L., Fussell, J. M., Hyde, C. E. & Crown, R. M. (1953). *J. Dairy Sci.* **36**, 593.
Rusoff, L. L., Fussell, J. M., Hyde, C. E., Crown, R. M. & Gall, L. S. (1954). *J. Dairy Sci.* **37**, 488.
Smith, W. M. (1954). *Vet. Rec.* **66**, 42.
Voelker, H. H. & Cason, J. L. (1951). *J. Anim. Sci.* **10**, 1065.
Voelker, H. & Jacobson, N. L. (1953). *J. Dairy Sci.* **36**, 592.

Choice of Diet by Rats

4. The Choice of Purified Food Constituents during Growth, Pregnancy and Lactation

By D. E. TRIBE

School of Veterinary Science, University of Bristol

(*Received* 21 *September* 1954)

Whether or not animals have the ability to select for themselves a diet capable of satisfying all their nutritional requirements is debatable. In many recorded experiments animals have been offered a variety of foodstuffs from which they could select their own diets, but the results have often been contradictory. For example, Evvard (1929) found that the food preferences of a pig varied with its degree of development and reflected in general terms the animal's physiological needs, but Braude (1948) concluded that it is essentially a matter of individual taste as to what ingredient of the diet is preferred by a pig. Pearl & Fairchild (1921) compared the egg production and body-weight gains of sixty chickens allowed free access to twelve common food materials with those of sixty birds fed on a standard poultry mixture. They concluded that chickens given freedom to choose the quantity and quality of their ration make a better physiological utilization of their ration than when kept under a system of controlled mass feeding, however excellent that system may theoretically be. Trials have been conducted to determine whether calves can be raised satisfactorily by allowing them choice of concentrates besides supplying milk and roughage (McCandlish, 1923*a*,*b*, 1924). These showed that calves and heifers, allowed free access to maize, oats, wheat bran, linseed meal and other protein supplements, will usually eat much more of the protein supplements than is required to balance their ration. Also, even if the animals choose freely from a mixture containing the correct proportion of protein supplements, after 2–4 months they will often eat an excess quantity

of protein and a deficient quantity of hay. Similarly, it has been shown by Nevens (1927) and Brown (1933) that lambs cannot be trusted to balance their rations if they are free to choose between maize and a protein supplement like linseed meal or cottonseed meal. Gordon & Tribe (1951) have reported that ewes failed to select throughout pregnancy a diet that enabled them to produce normal lambs.

However, all such experiments as these have been criticized by Richter, Holt & Barelare (1938) on the grounds that only mixed foods were employed and that to test appetite behaviour a choice between purified materials is essential. These authors consequently offered the following substances in separate containers to eight rats: olive oil, sucrose, cod-liver oil, wheat-germ oil, yeast, sodium chloride, calcium lactate, sodium phosphate and potassium chloride. All the animals made selections conducive to normal growth and reproduction. They grew as rapidly and were as active as animals on a standard McCollum diet and showed strikingly regular oestrous cycles. They mated, gave birth to litters of normal size and nursed them until the time of weaning. On the other hand, Kon (1931) failed to demonstrate any ability on the part of the rat to select an adequate diet when offered purified components on a free-choice system. Similarly, Scott (1948) in a series of experiments offered rats a choice of sucrose, casein, hydrogenated fat and mineral salts and reported results appreciably different from those of Richter *et al.* (1938), and Scott, Smith & Verney (1948) could find no relation between the food preferences of rats and age or pregnancy.

The experiment reported here was designed to determine whether rats in different physiological conditions (rapid growth, pregnancy and lactation) were able to select an adequate diet when offered seven basic dietary components on a free-choice system.

A brief account of some aspects of the investigation was communicated to the Physiological Society (Tribe, 1954).

EXPERIMENTAL

Management of rats

Fifteen female rats, each of which weighed about 100 g, were placed in individual cages measuring $24 \times 16 \times 8$ in. Wired around the walls of each cage were seven food containers that each contained one of the following foods—maize starch, glucose, margarine, yeast, casein, McCollum's salt mixture no. 185 and cod-liver oil. All the feeding pots were identical in shape and colour, and their positions in the cage were altered every 2nd day in order to nullify any possible effect of 'positional eating' by the rat. The amounts of the various foods on offer were recorded every 2nd day and the difference between these amounts and the bi-daily residues were taken as the quantities actually consumed. Beneath the meshed floor of each cage was placed a sheet of paper to collect any scattered food, but it seldom amounted to an appreciable quantity. All the animals were weighed twice weekly and received tap water without stint.

Arrangement of experiment

The experiment lasted for 16 weeks and is best considered in four distinct experimental periods.

Period 1. During the first 6 weeks the fifteen female rats, which since weaning had been fed on Rowett Institute stock rat diet (Thomson, 1936), were managed as described above and their choice of diet while adult although still increasing in body-weight was thus recorded.

Period 2. At the end of period 1 all the rats were mated and their selection throughout the 3-week period of pregnancy was recorded.

Period 3. In the next 3-week period the choice by all rats throughout lactation was recorded.

Period 4. Ten rats, five males and five females, were selected at weaning from the first generation produced by the original fifteen females and were maintained under the experimental management already described. In this way a record was obtained of food preferences during 4 weeks of active growth.

RESULTS

Period 1. Initially many of the fifteen rats failed to select a diet that enabled them either to increase or maintain their body-weights. With two exceptions, however, they soon increased both the quantity of food consumed and the percentage of protein in the diet, and over the whole 6-week period each rat made an average increase of 11 g/week in its body-weight. The two exceptions failed to select a diet capable of maintaining their body-weights and thus declined for 5 weeks and then died. A post-mortem examination confirmed that the deaths were due to starvation. Table 1 shows the average weekly consumption of food over the whole period for the group of thirteen rats alive at the end of it. By comparison mean weekly values for the remaining two rats were, for the period up to their death, food consumption 71 g, total calorie intake 263 Cal., percentage of total calories as protein 4, percentage of total calories as fat 29. All the calorific values have been calculated on the assumptions that 1 g maize starch ≡ 3·5 Cal.; 1 g margarine ≡ 7·3 Cal.; 1 g glucose ≡ 3·7 Cal.; 1 g yeast ≡ 3·5 Cal.; 1 g casein ≡ 3·8 Cal.; 1 g cod-liver oil ≡ 9·0 Cal.

Table 1. *Period* 1. *Mean individual weekly food intakes chosen by the thirteen female rats that survived period* 1

Week no.	Food consumption (g)	Calorie intake: Total (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
1	81	317	10	37	11
2	87	396	11	30	7
3	121	467	15	24	6
4	116	450	18	20	8
5	118	443	21	20	7
6	98	403	18	21	5
Mean	103	413	15	25	7

In no instance did a rat completely ignore any foodstuff, and the behaviour of the thirteen surviving animals was closely similar. They readily consumed both maize starch and glucose and did so in approximately equal quantities. The margarine was eaten in large amounts, particularly at first, when it contributed over one-third of the

total calorie intake. Yeast was distinctly more palatable than casein, but after a few weeks many rats seemed to acquire a taste for the latter.

Period 2. Although at the end of period 1 all thirteen does were caged individually with a buck, only ten of them were successfully mated and the following results therefore apply only to those ten. Table 2 gives the average weekly food intake selected by the group during the 3 weeks of pregnancy. At parturition there was produced an average of 8·5 young/litter of which 1·1 were stillborn, with an average birth weight of 5·0 g/rat.

Table 2. *Period* 2. *Mean individual weekly food intake chosen by ten pregnant rats*

Week no.	Food consumption (g)	Calorie intake: Total (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
1	120	497	18	25	5
2	128	547	18	31	6
3	110	494	17	36	3
Mean	119	513	18	31	5

Table 3. *Period* 3. *Mean individual weekly food intake chosen by ten lactating rats*

Week no.	Food consumption (g)	Calorie intake: Total (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
1	120	540	15	31	3
2	158	704	19	29	4
3	165	742	25	26	5
Mean	148	662	20	29	4

Table 4. *Period* 4. *Mean individual weekly food intake chosen from weaning until death by eight rats that died during the experiment*

Week no.	Food consumption (g)	Calorie intake: Total (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
1	59	182	1·6	20	2
2	32	125	1·6	22	0·2
3	24	90	1·1	19	0·3
4	26	62	1·5	26	0·5
Mean	30	115	1·5	21	0·7

Period 3. Table 3 gives the average weekly food intake selected by each rat during the 3 weeks of lactation. All the rats born were left with their mothers, but the average number weaned per litter was only 4·2, the remainder having been eaten by the does. Cannibalism took place in every litter. The average weaning weight for the survivors was 35·6 g.

Period 4. At weaning time ten of the forty-two surviving rats were individually caged and immediately introduced to the self-selection system of feeding. Records

of food selection were made during the next 4 weeks, by which time eight rats had progressively lost weight and eventually died. The average weekly food intake of these rats is shown in Table 4. The remaining two rats had increased in weight by an average of 10 g weekly during the same period and their average weekly food selections are shown in Table 5. The experiment was terminated at this point.

Table 5. *Period* 4. *Mean individual weekly food intake chosen after weaning by two rats that survived*

Week no.	Food consumption (g)	Calorie intake: Total (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
1	41	170	8·8	38	2·6
2	53	302	6·0	28	2·3
3	64	246	9·3	33	1·4
4	59	226	6·6	35	1·5
Mean	54	211	7·7	33	1·9

DISCUSSION

Period 1. The diets selected by the majority of the rats during this period showed a surprising similarity to those generally recommended for use as stock diets in small-animal laboratories. Table 6 compares the usual type of diet fed to such rats with the diets selected in this experiment. From these figures it will be noticed that the percentage of the total calorie intake in the form of protein was 15 for both, but the self-selection diet contained a higher percentage of calories derived from fat than did

Table 6. *Comparison of nutrients provided by the normal stock diet used at the School of Veterinary Science, University of Bristol, with those chosen in period* 1 *by rats during late growth*

Diet	Weekly food consumption (g)	Calorie intake: Weekly (Cal.)	Calorie intake: As protein (percentage of total)	Calorie intake: As fat (percentage of total)	McCollum's salt mixture no. 185 (g)
Stock	105	367	15	15	5
Selected	103	413	15	25	7

the normal diet. This higher fat intake accounts for the high calorie density/g of the chosen food. However, the fact that two out of fifteen animals failed to select a diet capable of maintaining life suggests the advantage of maintaining animals under a system of obligatory eating of a diet prescribed on the basis of known requirements.

Periods 2 *and* 3. There are two main ways of deciding whether a self-selected diet is adequate to meet an animal's needs. The performance of the animal on the diet can be measured, or the composition of the diet can be compared with that considered by nutritionists to be optimal. First, the performance of these rats during pregnancy and lactation may be compared with that of rats maintained by an orthodox method of feeding (Nelson & Evans, 1947). This comparison is made in Table 7. These figures show that, although the performance at parturition was almost precisely the same on

the two régimes, the percentage of the young weaned, and the survivors' body-weights, were very much inferior in the group choosing freely. This result can be accounted for on theoretical grounds by references to Tables 2 and 3. According to Murray

Table 7. *Periods 2 and 3. Comparison of the breeding performances of stock rats (Nelson & Evans, 1947) and of the ten rats which chose their own diets throughout pregnancy and lactation*

Rats	Average no. born/litter	Average birth weight (g)	Average no. born dead/litter	Average weight at 21 days (g)	No. weaned at 21 days (%)
Stock	8·8	6·0	0·2	48·0	90
Experimental	8·5	5·0	1·1	35·6	50

(1941) and Slonaker (1927) the food intake of pregnant rats increases by as much as 2–3·5 g/day. In this experiment the rats actually chose less food (and fewer calories) in the 3rd week of pregnancy than they did during the 1st week. However, as their initial food consumption was high (about 17 g/day), this probably means that the growth of the foetuses was unimpaired, but that the mammary development suffered in consequence. This would be reflected in the poor performance at weaning. In terms of food Slonaker (1927) has estimated a requirement of 20 g of food/pup during gestation and 71 g/pup during lactation. Since in the present experiment an average of 8·5 pups was born per litter and one-half of these were weaned, this represents a requirement over normal of 170 g during pregnancy and 355 g during lactation. Thus, since an average of 103 g of food was consumed per week before pregnancy (and this was close to the estimated normal), it means that, to satisfy the theoretical requirements, the rats should have consumed 489 g during pregnancy and 664 g during lactation. The consumption figures were 358 g in pregnancy and 443 g during lactation. In fact these calculations presuppose a calorific value of just under 4 Cal./g food, whereas in this experiment the calorific density was rather higher than this. Therefore the theoretical requirements were 1916 and 2656 Cal. for pregnancy and lactation respectively, and the consumption was 1538 and 1986 Cal. during pregnancy and lactation respectively. In addition to a deficiency of energy in the self-selected diets there was also a possible deficiency of protein. According to McCoy (1949), in his review of the nutritional requirements of rats, best reproduction and lactation occur on diets containing 25–30% protein, with possibly even better reproduction on a ration containing 40% protein. In this experiment the rats selected an average of 18% protein during pregnancy and 20% protein during lactation. It is of interest to note that before pregnancy only 15% protein was chosen, but it is doubtful if this tendency towards increased protein is significant, since in the first 5 weeks of period 1 (Table 1) the percentage protein increased from 10 to 21; thus it is possible that the rats acquired a taste for yeast and casein and that the increase is of no nutritional significance. Incidentally, the animals always ate more yeast than casein, and it is probable that if only casein had been presented the rats would have lost weight and died, as did those of Scott *et al.* (1948) in similar circumstances.

The theoretical requirements for rats during pregnancy and lactation have never been settled. The experimental literature is confused and contradictory (Russell,

1948) and it is therefore impossible to comment on the voluntary consumption of fat by these rats except to say that their intakes were unusually high. Again, however, this was probably merely a matter of palatability.

It is well known that an animal's requirement of major and minor nutrients increases during pregnancy and growth. In this experiment, however, the average weekly consumption of McCollum's salt mixture no. 185 declined from 7 g before pregnancy to 5 g during pregnancy and 4 g during lactation. Again this decline in consumption is reflected in the 6 weeks of period 1 (see Table 1), and is probably a matter of palatability and not of nutritive value.

Period 4. The disastrous performance of the young rats during period 4 is similar to that of similar rats studied by Kon (1931) on a self-selection system of feeding. As in Kon's experiments the most noteworthy feature was the voluntary limitation by the freely choosing rats of their protein intake, which was well below the standard accepted as necessary for the rat (see Table 4). Even the two rats that survived selected only 7·7% protein and their body-weight increases were subnormal.

SUMMARY

1. A study has been made of the ability of fifteen hooded Lister rats to select their diet when given a choice of the following foods: maize starch, glucose, margarine, yeast, casein, McCollum's salt mixture no. 185 and cod-liver oil.

2. If introduced to the free-choice routine when weighing approximately 100 g most rats selected a diet similar in composition to those generally recommended for use as stock diets, although two out of fifteen rats failed to thrive and eventually died.

3. During pregnancy and lactation the diets selected were deficient in both calories and protein and did not enable the does to rear normal litters.

4. When introduced to the routine at weaning, young rats were totally unable to select suitable diets and almost all died.

REFERENCES

Braude, R. (1948). *Bull. Inst. Study Anim. Behav.* no. 6, p. 17.
Brown, W. (1933). *Mich. Quart. Bull.* **16**, 3.
Evvard, J. M. (1929). *Res. Bull. Iowa agric. Exp. Sta.* no. 118.
Gordon, J. G. & Tribe, D. E. (1951). *J. agric. Sci.* **41**, 187.
Kon, S. K. (1931). *Biochem. J.* **25**, 473.
McCandlish, D. (1923*a*). *J. Dairy Sci.* **6**, 500.
McCandlish, D. (1923*b*). *J. Dairy Sci.* **6**, 572.
McCandlish, D. (1924). *J. Dairy Sci.* **7**, 160.
McCoy, R. H. (1949). In *The Rat in Laboratory Investigation*, 2nd ed. [J. Q. Griffith Jr. & E. J. Farris, editors.] London: Lippincott and Co.
Murray, G. N. (1941). *Onderstepoort J. vet. Sci.* **16**, 331.
Nelson, M. M. & Evans, H. M. (1947). *Arch. Biochem.* **12**, 213.
Nevens, W. B. (1927). *Bull. Ill. agric. Exp. Sta.* no. 289.
Pearl, R. & Fairchild, F. E. (1921). *Amer. J. Hyg.* **1**, 253.
Richter, C. P., Holt, L. E. Jr. & Barelare, B. Jr. (1938). *Amer. J. Physiol.* **122**, 734.
Russell, F. C. (1948). *Tech. Commun. Bur. Anim. Nutr., Aberd.*, no. 16.
Scott, E. M. (1948). *Trans. Amer. Ass. Cereal Chem.* **6**, 126.
Scott, E. M., Smith, S. J. & Verney, E. L. (1948). *J. Nutr.* **35**, 281.
Slonaker, J. R. (1927). *Amer. J. Physiol.* **83**, 302.
Thomson, W. (1936). *J. Hyg., Camb.*, **36**, 24.
Tribe, D. E. (1954). *J. Physiol.* **124**, 64*P*.