EXPERIMENTS ON THE FOOD PREFERENCES OF WILD RATS (*RATTUS NORVEGICUS* BERKENHOUT)

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(With 1 Plate and 9 Figures in the Text)

CONTENTS

(1) INTRODUCTION

This paper describes preliminary studies of the food preferences of closed colonies of wild *Rattus norvegicus* Berkenhout, kept in conditions resembling a normal habitat. It deals especially with their selection of cereals and cereal mixtures. The general behaviour of the rats of these colonies has been described elsewhere (Barnett & Spencer, 1951). The results are reported now because facilities for this work are no longer available.

(2) METHODS AND MATERIALS

Each colony consisted initially of ten to eighteen adult rats, of both sexes, which had been caught in cage traps in various environments. The numbers increased by breeding during the experiments, to a maximum of thirty-seven. The building used to house the colonies had formerly been stables. It was divided into seven rooms, each rat-proofed and supplied with a nesting place of biscuit tins and sacking, and a water point (Pl. 1, Fig. 1). During all experiments the rats had a surplus of cereal food; they also received a supply of cabbage once a week and of horse liver once a fortnight.

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Fig. 1.

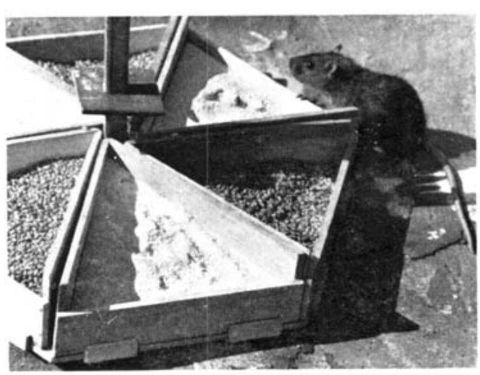


Fig. 2.

In each experiment except two the rats were offered a choice of two cereals or mixtures in a tray with six compartments (Pl. 1, Fig. 2). The two foods were put in alternate compartments and the amount in each was weighed daily to the nearest 5 g. In the two exceptional experiments, in which there was a choice of three foods, food A was put in compartments 1 and 4, food B in 2 and 5 and food C in 3 and 6. The tray was always put in the same place but the precise positions of the different foods in relation to the room varied at random from day to day. Apart from the cabbage and liver, the only food available was that in the tray. The materials used are shown in Table 1. Each experiment was given a reference number; for

Table 1

Foodstuff	Description	Proportions used in mixtures, by weight
Whole wheat	English, large grained white variety	—
Wheat germ	Commercial*	—
Wholemeal	93 % extraction*	—
White flour	Canadian, about 75 % extraction, fortified*	—
Rusk	Unleavened biscuit meal†	Damp rusk contains 1:1 rusk and water
Castor sugar	—	With wholemeal: 10 %; with white flour: 10 % unless otherwise stated
Saccharin	—	0·033 %
Cod-liver oil	Vitamin A 1007 i.u./g., Vitamin D 119 i.u./g.	2·5 g. oil to each 100 g. wheat
Arachis oil	Refined, deodorized	2·5 g. oil to each 100 g. wheat; 30 g. oil to each 100 g. wholemeal or wholemeal and sugar mixture
Cabbage	—	—
Horse liver	—	—

* Results of analyses carried out by Cereals Research Station:

Foodstuff	Ash (%)	Fibre (%)	Vitamin B_1 (i.u./g.)
Wholemeal	1·23	1·44	1·15
White flour	0·52	0·12	0·95
Wheat germ	4·37	1·91	5·5

† Composition of 100 g. dry rusk: water, 14·0 g.; protein, 11·0 g.; fat, 1·0 g.; carbohydrate (from wheat flour), 68·0 g.

example, the first experiment in room 4 is numbered 4/1, and the seventh experiment in room 1 is numbered 1/7. These reference numbers are shown on the text-figures, which give graphically the results of some of the experiments, and in Table 2.

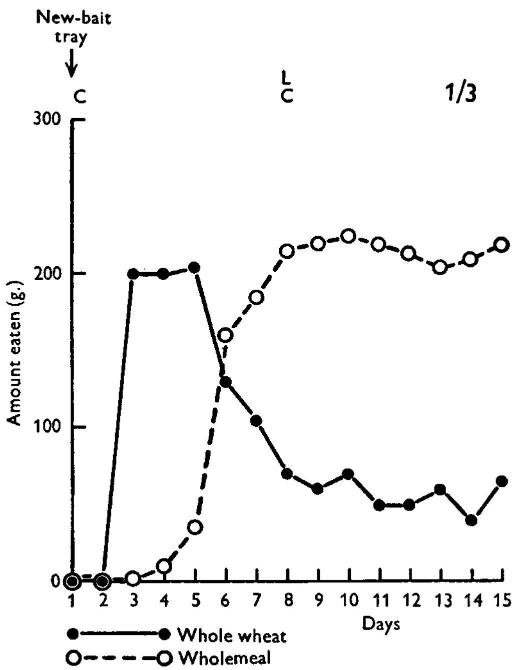
Table 2 summarizes the experiments. The experiments on each rat colony (i.e. in each room) followed each other without an interval. As a rule a particular choice, such as between white flour and whole wheat, was offered to several different colonies at different times. Sometimes a choice was offered a second time to a colony after an interval of some weeks. Nine experiments are omitted from this account but are described elsewhere (Barnett & Spencer, 1952).

(3) RESULTS

(a) *Plain cereal foods*

These are the results of tests on whole wheat, wholemeal, wheat germ, white flour and dry rusk. The last is not strictly a plain cereal food, but it is convenient to include it here.

(i) Wholemeal was regularly preferred to whole wheat in three tests. In the first two tests the rats had no previous experience of wholemeal, and the preference developed only after several days (Text-figs. 1, 2).



Text-fig. 1. Wholemeal preferred to grain. Change of preference reflects previous feeding on grain only. No intake for first 2 days due to avoidance of unfamiliar bait tray (cf. Chitty & Shorten, 1946).

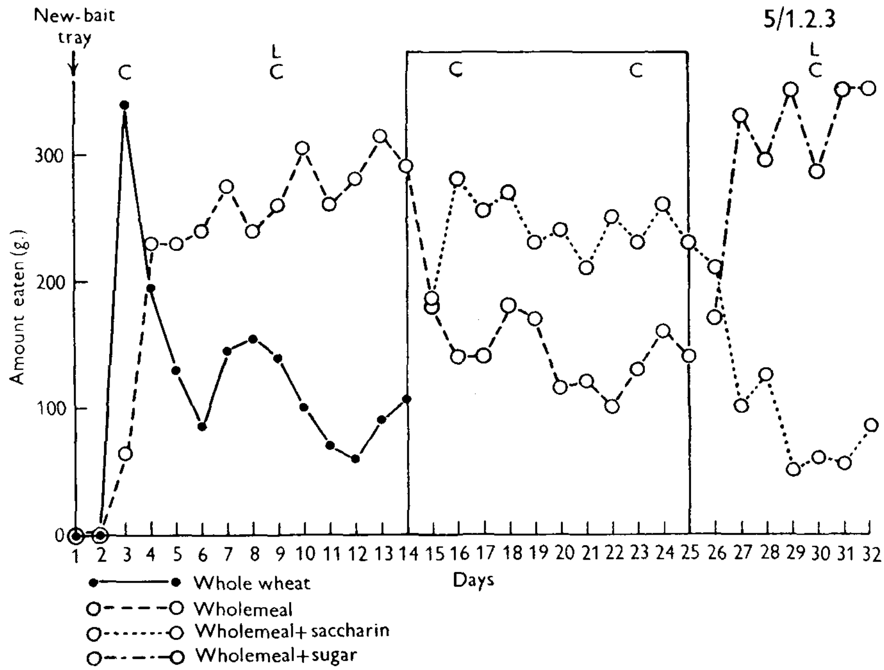
Explanation of figures. The daily intake is shown for each food to the nearest 5 g. Where appropriate, the results of successive experiments are shown in the same figure. Experiment numbers are shown on each figure, with the number of the room first.

C = cabbage; L = liver. These letters are inserted opposite the intake for the day after that on which the cabbage or liver was put in the rooms.

In some instances (e.g. Text-figs. 1 and 2), introduction of a new bait tray caused a temporary reduction in intake, and this is indicated at the top of the figure.

(ii) When, instead of wholemeal, a choice of white flour and whole wheat was offered, the latter was in general preferred (Text-figs. 3, 4). In one experiment (4/2) several days were required before the preference became evident, probably because the colony had previously been feeding largely on white flour. In a fourth experiment (1/9) the rats had been feeding largely on white flour and sugar with some wheat germ; they had then been given whole wheat alone for 15 days; after this they ate slightly more white flour than wheat.

(iii) In four experiments a clear preference was shown for wholemeal over white flour (Text-fig. 3). This occurred whether the colonies had previously been fed on wheat or on white flour. The preference was shown immediately. The amount of white flour eaten was small and declined with time almost to nothing. A similar decline was shown also in one experiment in which white flour was given with whole wheat (Text-fig. 4).



Text-fig. 2. As Text-fig. 1. Shows also preference for sweet mixtures, and for sugar rather than saccharin. Each change of diet involves an initial change of choice.

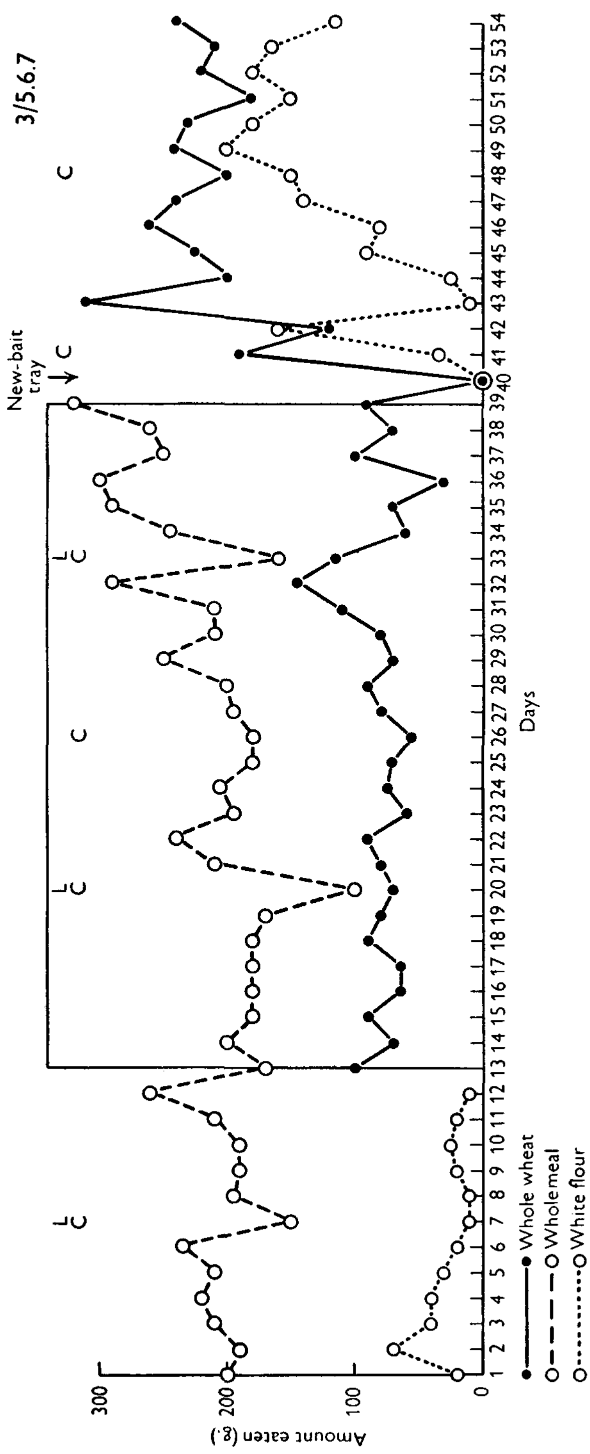
(iv) Both wholemeal and white flour were preferred to wheat germ, and very little wheat germ was eaten in these experiments. This result may be compared with the experiments, described later (*b*, vii), in which the choice was offered between sugar mixtures or sugar itself and wheat germ: in the latter the intake of wheat germ was higher.

(v) In two experiments the choice was offered between dry rusk and wholemeal. In the first experiment almost equal quantities of the two foods were eaten. In the second experiment, done with rats which had been given rusk mixed with water in a previous experiment, a marked preference was shown for wholemeal rather than the dry rusk.

(*b*) *The effects of sweetness*

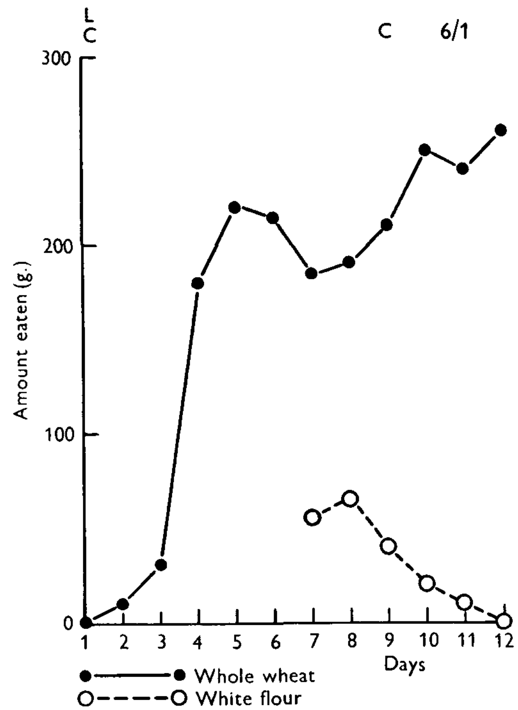
In these experiments sugar or saccharin was added to cereals.

(i) In two experiments white flour plus sugar was clearly and immediately preferred to wholemeal alone (Expts. 2/11, 7/11; Text-fig. 5). The addition of sugar to white flour thus reversed the preference described in paragraph (*a*, iii).



Text-fig. 3. Wholemeal (which had already been experienced) preferred at once to white flour and, less markedly, to whole wheat. Whole wheat, however, was slightly preferred to white flour. Ingestion of liver caused a differential decline in the amount of wholemeal eaten (days 7, 20, 33).

(ii) Each of the two preceding experiments was followed by one in which the choice was offered between wholemeal plus sugar and white flour plus sugar. In one (Expt. 7/8) there was an immediate and clear preference for the wholemeal mixture. In the other (Expt. 2/12), although the amount of wholemeal plus sugar eaten increased compared with that of the wholemeal alone in the previous experiment, the habit of eating mainly white flour plus sugar persisted.



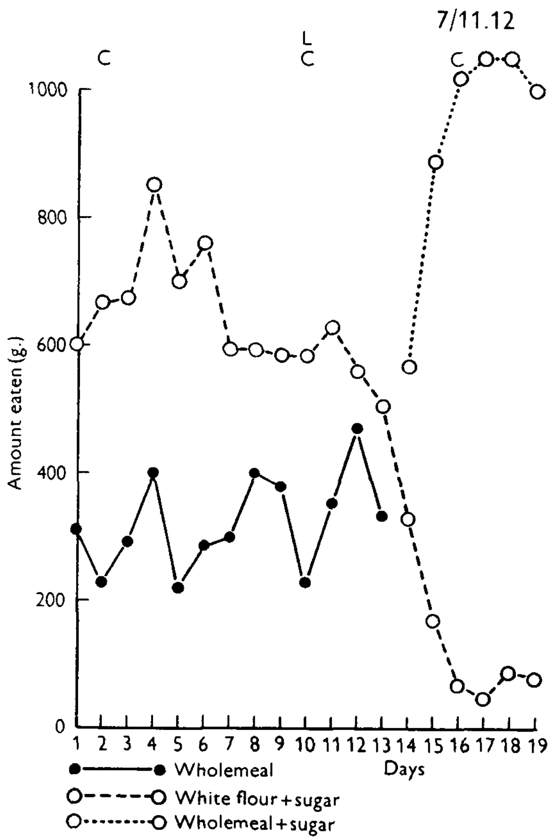
Text-fig. 4. Whole wheat markedly preferred to white flour. Decline in amount of white flour eaten, as in Text-fig. 3, Expt. 3/5.

(iii) Two tests compared wholemeal plus sugar with dry rusk. In one (Expt. 4/14) the rusk was eventually preferred, after 6 days during which no marked preference was shown. In the other (Expt. 5/9) there was a clear preference for the wholemeal mixture. These rats had previously been fed on rusk mixed with water (cf. *a*, v).

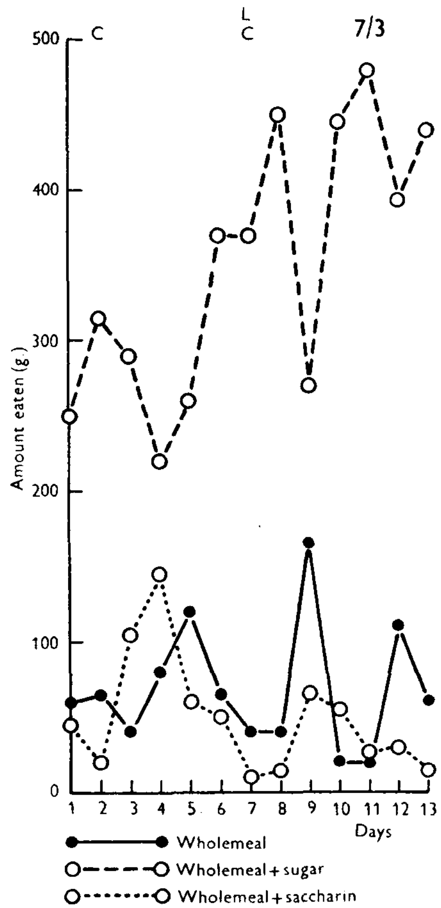
(iv) Four tests compared wholemeal with wholemeal plus saccharin. In two (Text-fig. 2) there was a consistent preference for the saccharin mixture. Colony no. 4 was used for both the other tests: in the first the result was a preference on the whole for the saccharin mixture, but there was a period of 4 days during which more plain wholemeal was eaten. In the later test on this colony the plain wholemeal was consistently preferred. The colony had been feeding largely on sugar for 13 days before this experiment.

(v) In two experiments wholemeal plus sugar was preferred to wholemeal plus saccharin (Text-fig. 2). This preference was confirmed in a third experiment (Text-fig. 6) in which wholemeal plus sugar was clearly preferred both to wholemeal and to wholemeal plus saccharin.

(vi) Soaked whole wheat plus sugar was compared with soaked whole wheat plus saccharin in three experiments. On the whole the sugar mixture was preferred, but the degree of preference for sugar was reduced when wet baits were used. In



Text-fig. 5.



Text-fig. 6.

Text-fig. 5. Effects of sweetness. Progressively more marked preference over first 3 days of Expt. 7/12.

Text-fig. 6. Sugar preferred to saccharin; but some of each of three foods eaten throughout experiment. Wholemeal + saccharin not preferred to wholemeal in these conditions. The daily fluctuations probably reflect the fact that three alternatives are available (see also Text-fig. 9).

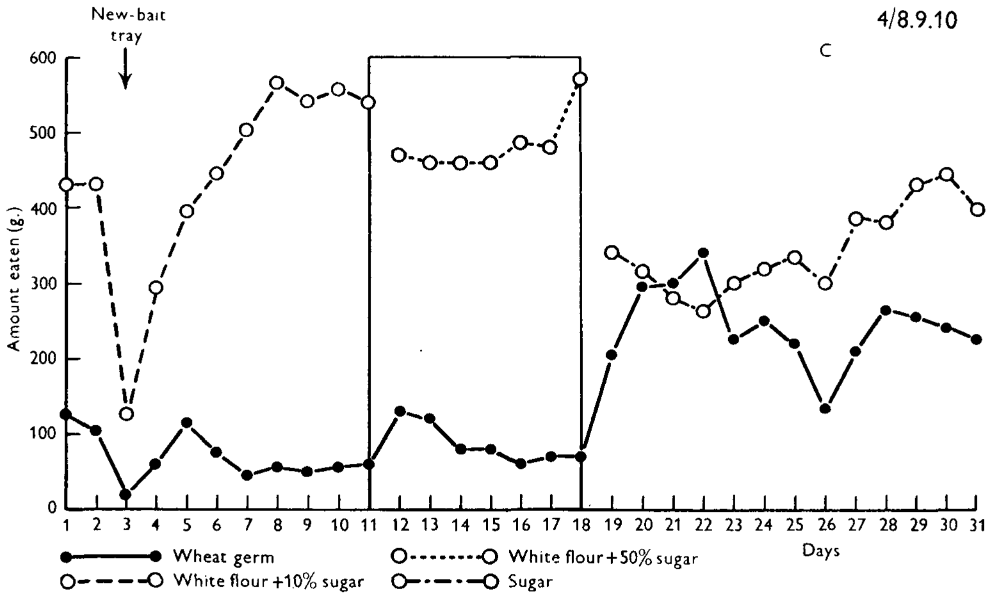
Expt. 6/5, however, the results were confused by the fact that after the first day the colony consumed completely the food in the compartment nearest the door, whichever mixture it contained (see *g*).

(vii) Sugar or sugar mixtures were compared with wheat germ in a series of experiments (Text-fig. 7). No liver was given during any of these experiments. The amount of germ eaten increased with the proportion of sugar in the alternative food.

(*c*) *The effects of oils*

These experiments illustrate the effects of the addition of arachis oil or cod-liver oil to wheat and wholemeal.

(i) A mixture of arachis oil with wheat was on the whole preferred to plain wheat. However, in Expt. 7/2 there was a period of 23 days during which no decisive preference was shown; the proportion of the arachis mixture eaten did, however, rise during this period and after the 23rd day there was a clear preference for it.



Text-fig. 7. Wheat germ intake rises when the only source of carbohydrate is sugar alone.

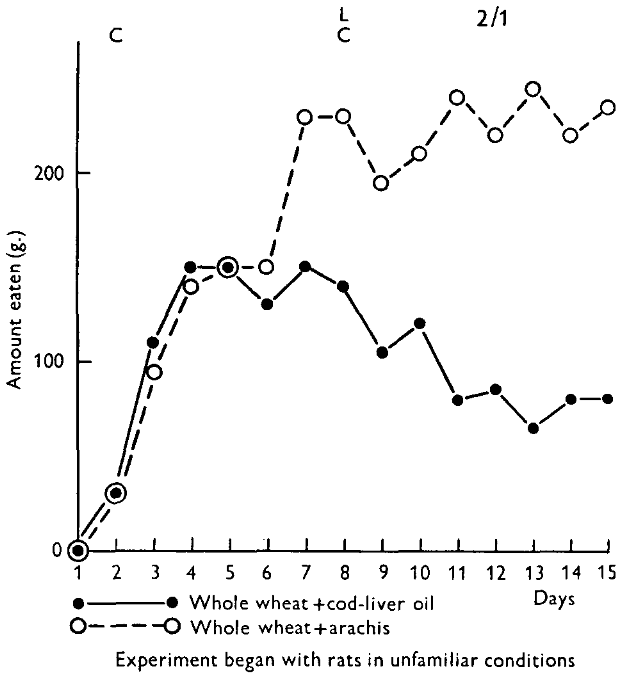
The experiment was repeated on the same colony 12 weeks later. Again the proportion of arachis mixture eaten rose, but the experiment had to be ended before a period of consistent preference was reached.

(ii) When the choice was offered between a mixture of wholemeal plus arachis oil and wholemeal alone, the mixture was consistently preferred, but considerable amounts of the plain wholemeal were eaten.

(iii) When wheat plus arachis oil was compared with wholemeal plus arachis oil the results were equivocal, but the wholemeal mixture was in general slightly preferred.

(iv) The effect of adding cod-liver oil to wheat was the opposite of that of adding arachis oil. In three out of four tests (1/1, 1/11, 4/3) the plain wheat was preferred, although the preference was not marked and, in Expt. 1/1, 21 days elapsed before a decisive difference appeared in the amounts eaten. In the fourth experiment (3/4) there was a very slight preference for the cod-liver oil mixture. In all experiments except 1/11 there was a tendency for the amount of cod-liver oil mixture eaten to decline with time.

(v) This decline in the proportion of cod-liver oil mixture eaten was shown also in one of the three experiments in which the choice was offered between wheat plus arachis oil and wheat plus cod-liver oil (Text-fig. 8). In all these experiments there was a decisive preference for the arachis mixture, but in two this preference was not shown at first. In the third experiment (1/2) the preference was consistently shown throughout. The colony which showed consistent preference had been feeding partly on a cod-liver oil mixture immediately before the experiment.



Text-fig. 8. Arachis oil preferred to CLO. By the fourth day they were eating a normal amount, and on days 4–6 no preference was shown. After this the intake of CLO mixture declined steadily, with a corresponding increase in consumption of the alternative.

(*d*) *Sweet and oily mixtures*

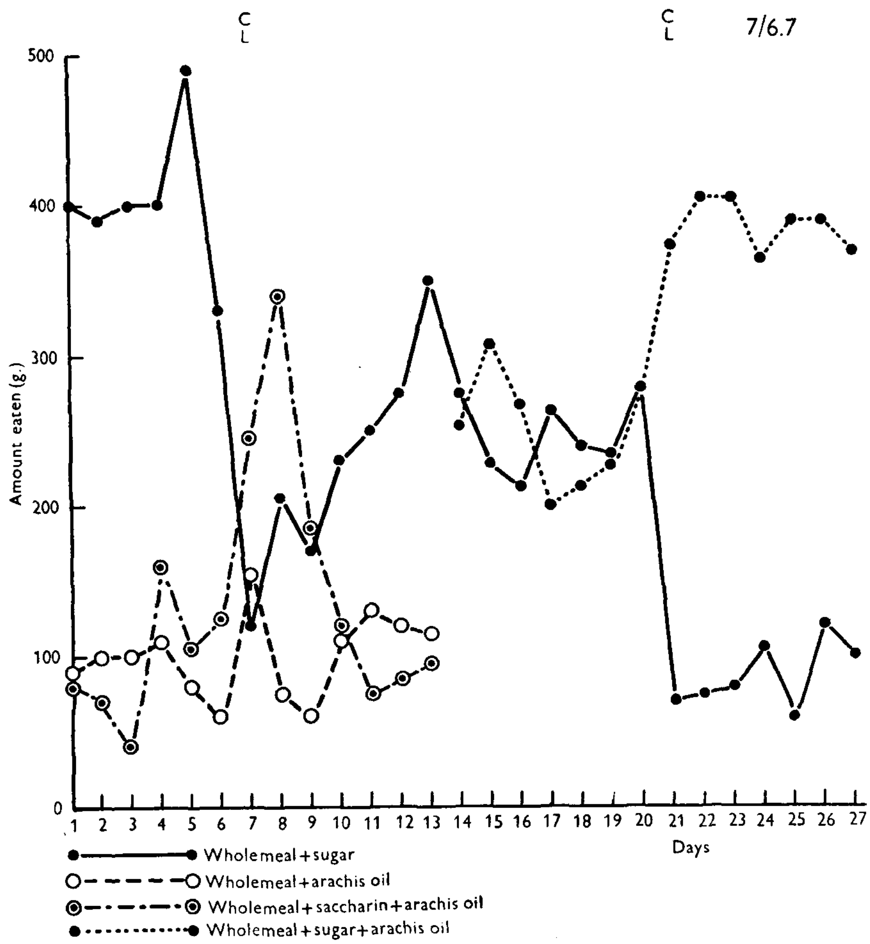
(i) In two tests the choice was offered between wholemeal plus arachis oil and wholemeal plus sugar. In one (6/7) the arachis mixture was preferred; in the other (4/12) the preference was for the sugar mixture.

(ii) After a number of tests it became clear that wholemeal was the preferred cereal and that the presence of arachis oil or of sugar tended to increase the acceptability of a mixture. Tests were therefore carried out with a mixture of wholemeal, arachis oil and sugar, and it was found that this mixture was on the whole preferred both to wholemeal plus sugar and to wholemeal plus arachis oil (Text-fig. 9).

(iii) When, instead of sugar, saccharin was used for the triple mixture (Expts. 2/7 and 5/6) there was no effect attributable to the presence of saccharin. This result was confirmed also in a test in which wholemeal plus arachis, and wholemeal plus arachis plus saccharin were offered, with wholemeal plus sugar as a third choice.

(*e*) *The effect of the ingestion of liver*

In the conditions of these experiments, liver was preferred to all other foods, though not to their complete exclusion. In some tests the consumption of liver affected the intake of the two other foods almost equally, but sometimes, as can



Text-fig. 9. Effects of arachis oil and sweetness. In Expt. 7/6, with three alternatives, each of the three was eaten, but wholemeal + sugar was clearly preferred to the other two. This preference was, however, upset on days 7–9, on the first of which liver was available. During these 3 days wholemeal + saccharin + arachis was preferred. In Expt. 7/7, for 7 days no preference was shown; but on the eighth day liver was given, and from that day a clear preference developed for wholemeal + sugar + arachis over wholemeal + sugar.

be seen from Text-figs. 3, 5 and 9, one food was conspicuously more affected than the other. In five experiments changes of preference were observed immediately after a day on which liver was supplied. Examples are given in Text-fig. 9. In Expts. 7/2 and 7/7 clear and persistent preferences developed after these changes took place, but in the other experiments the changes were temporary.

(*f*) *Deterrent effect of stale flour mixtures*

Usually flour or flour mixtures which remained after 24 hr. were not discarded after weighing but were put back in the trays after being made up with fresh material to the necessary weight. Sometimes one compartment of the tray contained fresh material and two other compartments a mixture of fresh and stale. In three experiments (1/8, 4/13 and 2/6) the fresh mixture was taken in preference to the stale. A similar effect was observed with flour and oil mixtures on an occasion when the supply of arachis oil was low and residues were mixed with fresh material to make up the necessary weight. In room 5 at this time there was a marked drop in the amount of food taken, whether measured in grams or in calories (5/6). A similar drop occurred in room 2 (2/7). In room 6 the wheat plus arachis oil mixture was freshly prepared, while the wholemeal plus arachis oil was not; this may have had some bearing on the result of this test, since the wheat mixture was preferred (6/3), whereas in other experiments on this choice the flour mixture was preferred.

(*g*) *Place preference*

In general, the preferred compartments of the food tray were those nearest to the wall or to the nest. This was nearly always so when the rats were directly observed while feeding (Barnett & Spencer, 1951). Sometimes, however, there were departures from this rule, and either a particular compartment was preferred, regardless of its position, or that compartment was preferred which was in a particular relationship to the rest of the room. In Expt. 1/7 and part of Expt. 1/8 wheat germ was taken from one tray only, regardless of its position. In Expt. 1/3 (Text-fig. 1) there was a preference for the compartments farthest from the nest; this preference did not seem to interfere with food choice. In Expt. 6/5 there was again a preference for the compartment farthest from the nest; in this instance the food from the preferred tray was always completely consumed whichever food it was. Similar preferences were observed in some other experiments reported elsewhere (Barnett & Spencer, 1952).

(*h*) *Influence of calorific value of food*

(i) The effect of the calorific value of mixtures was shown in experiments in which damp rusk was compared with dry or oily alternatives. When damp rusk was compared with wholemeal there was a very marked preference for the rusk in terms of the weights eaten. When the calorific values were compared, there was still a preference for the rusk in one experiment (2/5), but in the other (4/5) each food accounted for 50 % of the total calorific intake. When the choice was offered between damp rusk and wholemeal plus sugar, the weight of rusk eaten was by far the greater in four out of five tests. In terms of calories, one colony showed a very slight preference for the rusk in two tests (5/8, 5/4); in two other tests (2/6, 4/7) the calorific values were approximately equal. In one test (3/13) there was a change after 3 days to a consistent preference for the wholemeal plus sugar, and this was sustained for the remaining 16 days of the test.

When the choice was offered between damp rusk and wholemeal plus arachis oil, although a much greater weight of rusk was taken there was in one test (5/5) a preference in terms of calories for the flour and oil mixture. In the other test (4/6) the calorific intake due to the flour and oil was about 75 % of that due to the rusk. This may be compared with the fact that the *weight* of damp rusk eaten was four times that of the weight of the flour and oil.

(ii) The constancy of calorific intake, regardless of the particular foods eaten, was shown in the records of intake of each rat colony studied as a whole. If the calorific value of the food eaten in each week is plotted against time a steady increase is shown, corresponding to the increase in biomass of the colony resulting from both breeding and individual growth. The numbers and weights of the rats were known only at the time when a colony was installed and when all the experiments with it were completed. From these figures it is possible to plot calorific intake against weight of rat colony; the curve shows a straightforward relationship in which calorific intake is approximately proportional to colony weight. This statement requires, however, at least one qualification. Calorific intake per unit weight varies with the weight of the rat. Thus if the mean weight of the rats in each colony is plotted against the food consumption expressed as calories per kg. of rat, the higher the mean weight of the rats, the lower is the calorific intake per kg. Other factors, such as activity, no doubt affect calorific intake, but are unlikely to have a marked effect on the intake of a whole colony.

(4) DISCUSSION

(*a*) *Problems of interpretation*

A common feature of choice experiments is that, even when there is a marked difference in the amount of two foods eaten, rats eat an appreciable amount of the less acceptable food. In our experiments this also occurred when three foods were offered. Thus rats are not only capable of feeding on a wide range of foods, but if many foods are available at one time, all are likely to be sampled. We have, however, little information about the behaviour of individual rats in a colony, and it is possible that there is individual variation in the selection of foods; but evidence presented elsewhere suggests that the majority of rats in a given colony all behave similarly in the selection of foods (Barnett & Spencer, 1951).

The omnivorous behaviour of rats leads to difficulties in expressing the results of preference experiments. If the less acceptable food was not eaten, or was eaten only in the proportion of, say, 5 % of the total intake, the presentation of results would be easy. As it is, the proportion may vary from 0 to 50 %, and this leads to the use of imprecise expressions such as 'marked preference' or 'slight preference'. We therefore show, in Table 2, the mean daily intake of each food in each experiment, and for selected experiments text-figures with the amounts of the foods eaten on each day. Table 2 presents the results also in terms of the calorific value of the foods eaten. Sometimes the weight of a food eaten, compared with that of an alternative, clearly reflected its different calorific value per unit weight. In other words 'preference' may be assessed in terms either of actual weight of

Table 2. *Mean daily intake for each test*

Test no.	g.	Cal.	% Cal.	g.	Cal.	% Cal.	Length of test (days)
		Wheat			Wholemeal		
1/3	87	295	38	140	489	62	15
5/1	115	391	35	214	739	65	14
3/6	81	273	27	213	737	73	27
		Wheat			White flour		
6/1	223	754	87	32	115	13	6
4/2	148	501	81	31	115	19	24
3/7	204	693	63	112	409	37	15
1/9	209	708	39	310	1130	61	14
		Wholemeal			White flour		
3/5	205	709	88	26	96	12	12
7/1	310	1071	79	78	285	21	18
2/3	219	758	82	47	171	18	13
4/1	226	782	95	11	40	5	14
		Wholemeal			Wheat germ		
1/5	243	842	86	38	142	14	9
3/9	335	1159	82	68	257	18	9
		White flour			Wheat germ		
1/6	261	953	92	21	78	8	12
3/10	361	1316	91	36	134	9	7
		Dry rusk			Wholemeal		
4/13	388	1260	51	344	1191	49	14
5/10	139	453	22	457	1581	78	8
		Wholemeal			White flour + sugar		
2/11	62	214	19	251	924	81	5
7/11	323	1118	32	639	2352	68	13
		Wholemeal + sugar			White flour + sugar		
7/12	931	3267	87	133	488	13	6
2/12	72	252	24	217	798	76	8
		Dry rusk			Wholemeal + sugar		
4/14	378	1229	56	279	981	44	9
5/9	86	278	15	466	1634	85	9
		Wholemeal			Wholemeal + saccharin		
5/2	143	495	37	240	830	63	11
7/8	191	660	29	469	1624	71	7
4/4	183	631	44	231	799	56	14
4/11	637	2204	83	129	445	17	7
		Wholemeal + sugar			Wholemeal + saccharin		
3/11	367	1288	89	45	154	11	10
5/3	304	1068	76	98	338	24	7
		Soaked wheat + sugar			Soaked wheat + saccharin		
3/12	489	1086	61	340	691	39	11
6/5	328	729	64	199	404	36	6
7/5	467	1037	56	403	818	44	9
		White flour + sugar			Wheat germ		
1/7	285	1050	91	28	106	9	16
4/8	440	1619	86	70	261	14	11
		White flour + 50% sugar			Wheat germ		
1/8	321	1217	82	72	271	18	17
4/9	484	1833	85	86	322	15	7
		Sugar			Wheat germ		
4/10	345	1359	60	243	915	40	13
		Wheat			Wheat + arachis		
3/8	61	205	17	291	1025	83	10
6/2	80	271	37	129	454	63	7
7/2	97	329	36	165	583	64	30
7/10	410	1390	54	338	1192	46	13

Table 2 (*cont.*)

Test no.	g.	Cal.	% Cal.	g.	Cal.	% Cal.	Length of test (days)
		Wholemeal			Wholemeal + arachis		
5/11	118	406	22	301	1427	78	10
6/6	39	133	17	141	670	83	7
		Wheat + arachis			Wholemeal + arachis		
1/10	251	885	49	192	910	51	13
6/3	216	763	76	52	247	24	9
7/9	239	845	31	397	1882	69	7
2/4	154	543	42	158	746	58	14
2/10	109	386	37	136	645	63	9
		Wheat			Wheat + cod-liver oil		
1/1	138	469	64	75	266	36	35
4/3	196	665	56	149	525	44	22
1/11	338	1144	63	190	671	37	8
3/4 (part)	93	316	44	115	406	56	14
		Wheat + cod-liver oil			Wheat + arachis		
2/1	97	344	36	173	609	64	15
3/15	267	941	38	426	1504	62	9
1/2	29	104	13	206	725	87	9
		Wholemeal + arachis			Wholemeal + sugar		
6/7	167	792	73	84	295	27	10
4/12	106	502	20	584	2050	80	5
		Wholemeal + arachis + sugar			Wholemeal + sugar		
2/9	172	820	64	133	465	36	10
6/4	168	802	81	55	193	19	12
7/7	297	1420	71	168	589	29	14
3/14	142	669	32	404	1417	68	13
		Wholemeal + arachis + sugar			Wholemeal + arachis		
2/8	150	719	58	112	531	42	12
5/7	209	1000	59	145	689	41	12
		Wholemeal + arachis + saccharin			Wholemeal + arachis		
2/7	112	532	48	122	577	52	9
5/6	141	670	48	153	724	52	11
		Damp rusk			Wholemeal		
2/5	544	882	61	162	559	39	9
4/5	686	1111	50	315	1090	50	6
		Damp rusk			Wholemeal + sugar		
5/4	709	1149	58	233	816	42	8
5/8	570	923	45	317	1111	55	6
2/6	390	632	50	179	629	50	7
4/7	674	1092	51	294	1031	49	8
3/13	303	491	25	410	1439	75	19
		Wholemeal + arachis			Damp rusk		
5/5	214	1016	54	524	849	46	8
4/6	164	778	42	659	1068	58	11

Test no.	g.	Cal.	% Cal.	g.	Cal.	% Cal.	g.	Cal.	% Cal.	Length of test (days)
		Wholemeal			Wholemeal + sugar			Wholemeal + saccharin		
7/3	68	235	14	350	1230	75	49	170	10	13
		Wholemeal + arachis + saccharin			Wholemeal + arachis			Wholemeal + sugar		
7/6	133	629	29	100	476	22	308	1083	49	13

food eaten or of calorific value of food eaten. Fortunately, in most of our experiments the calorific values of the two alternative foods were similar.

(b) Factors influencing choice

The factors which influence the selection of food by rats may be provisionally classified under four headings:

(i) palatability (flavour) of food;
(ii) nutritional value of food;
(iii) previous experience of rats (food habits);
(iv) position of food.

(i) The *palatability* of a cereal food is increased by sweetening agents and probably by oils with no very marked taste. In our experiments there was a general tendency to prefer sweet to non-sweet foods, whether the sweetening agent was sugar or saccharin. Adolph (1947) found that materials without nutrient value had little effect on the preferences of white rats: saccharin, in particular, led to hardly any significant increase in intake. This is evidently a point on which wild rats differ from laboratory strains. Our results show that there are several such differences.

The effect of adding arachis oil was similar to that of adding sugar. On the other hand, the addition of cod-liver oil tended to have a deterrent effect. Scott & Verney (1948) report analogous preferences in white rats. It might be thought that the addition of both arachis oil and sugar would produce an especially acceptable mixture, but in fact the two together had only slightly more effect than one separately. Cameron (1947) refers to the depression for sweetening agents of the effects of the taste receptors in man caused by the presence of other, non-sweet stimuli; this may have occurred in our experiments.

Apart from flavour, state of division and softness of foods may influence preference (Carlson & Hoelzel, 1949; Spencer, 1953). In our experiments this was probably responsible for the clear preference shown for wholemeal over whole wheat.

(ii) That *nutritional value* influences the total intake of a food can be demonstrated by estimating the calorific value of the food eaten. Rats and other animals regulate their feeding to balance their energy requirements (Hausmann 1932, 1933). A difficult question is whether rats also regulate their food intake in relation to their needs for amino-acids, salts or vitamins. Our own experiments were not designed to give evidence on this question, but some of the results suggest 'dietary self-selection'. The results with wheat, wholemeal and white flour possibly demonstrate this. Whereas wholemeal was preferred to wheat, presumably for its state of division, white flour was *not* preferred to wheat. Although the influence of flavour cannot be ruled out (Neuhaus, 1950), the repeatedly observed decline in the consumption of white flour suggests a process of learning to avoid white flour and to eat the superior form of cereal in preference. An ability to select foods containing B vitamins (Scott & Quint, 1946; Scott & Verney, 1947*b*) may also have influenced the results of our experiments with wheat germ. Wheat germ, which has a high content of B vitamins (Table 1), was offered as an alternative to mixtures of white flour and sugar, or sugar alone. When the alternative to wheat germ was white flour plus 10 % sugar, the intake of germ was very low, but when sugar alone was offered the amounts of sugar and wheat germ eaten were nearly equal (Text-fig. 7).

The obverse of the selection of more valuable foods is the refusal of harmful materials (Armour & Barnett, 1950). A possible example is the decline which took place in the intake of cod-liver oil mixtures. Hypervitaminoses A and D are well known (Harris & Moore, 1928; Moore, 1949), and might account for this phenomenon. A distinction must be made between a consistent refusal of a cod-liver oil mixture (which, as we have seen, is likely to be due to the flavour of the oil) and a trend from a high to a low intake, which suggests a toxic effect. However, none of our experiments enables us to distinguish with certainty between an effect of flavour and one of nutritional value.

(iii) The most notable of the effects observed were those of the *previous feeding experience* of the rats. These phenomena are comparable with those described in man as 'food habits'. 'Previous feeding experience' may refer here either to the effect of feeding in previous experiments, or to the effect of feeding early in an experiment on behaviour in its later stages.

The best examples of the effect of food eaten before an experiment began are those in which there was a change of preference. In two experiments (Text-figs. 1 and 2) the rats had been feeding on wheat only. When they were offered the choice of wheat or wholemeal they at first ate wheat and little or no meal, but after a few days they had changed their preference largely to wholemeal. A similar effect was seen in one experiment in which a choice was offered between whole wheat and white flour after the rats had been accustomed to eating only flour (white or wholemeal) for some weeks. For the first 4 days the small amount of food eaten was almost entirely white flour, but thereafter whole wheat was preferred. In another instance (Text-fig. 2, Expt. 5/3) rats which had been feeding largely on wholemeal plus saccharin showed a slight preference for this mixture over wholemeal plus sugar on the first day, but afterwards ate very little of the saccharin mixture.

These are clear examples. It is likely that such effects influenced other choices also. They are in contrast to the behaviour of the white rats which often 'appeared to relish a change in the carbohydrate portion of their ration' for 1 or 2 days (Scott & Verney, 1947*a*).

In some experiments a definite preference was eventually established only after a period of fluctuation in the amount of each food eaten. This was observed in three experiments (1/1, 3/4, 4/10) in which one of the foods contained cod-liver oil (Text-fig. 8). It did not occur in all experiments with cod-liver oil and was quite absent from one experiment (1/11); in another (3/15) there was only a change in preference after the second day. Another example of a delay in the establishment of preference is given in Text-fig. 9. The delays were sometimes long: in Expt. 7/2, 22 days elapsed before a preference became evident, and in one of the cod-liver oil experiments (1/1) the delay was 21 days. Much more investigation is needed for a satisfactory interpretation of these results.

In the experiments mentioned in the preceding paragraph there was a tendency for the amount eaten of the less acceptable food to decline steadily with time after the period of indecision. A similar steady decline was, as we have seen, observed in other experiments, even though there was never any doubt which of the two foods was preferred. In three experiments (6/1, 7/1 and 2/3) the intake of white flour showed such a decline (Text-fig. 4), while in other experiments the intake of white flour was negligible. As we have seen, this progressive refusal of a particular food may be a process of learning to avoid a slightly toxic food.

A feature of some of the experiments mentioned in this section is the erratic intake of each food from day to day. When no decisive preference was being shown it was rare for the daily intake of the two foods to remain steady at about 50 % of the total. (In this respect Expt. 2/1, Text-fig. 8, was atypical.) The situation in such an experiment seems to be analogous to that in experiments, described by Miller (1944), on 'approach-approach competition' in white rats. Miller describes such a situation as one of unstable equilibrium, in which quite trivial variations in conditions, e.g. the relative positions of two foods offered, might cause marked changes of apparent preference.

(iv) The fourth factor, the *position* of the foods in relation to other parts of the environment, is a minor one, but of practical importance both for the design of experiments and for rat control in the field. 'Place preference' has been observed by Chitty (unpublished) in the field, and 'container preference' is mentioned by Scott (1946) in an account of experiments on laboratory rats. As we have described, such effects were evident in some of our experiments, but it seems that in most there was no significant place-preference effect.

SUMMARY

1. Colonies of wild *Rattus norvegicus* Berkenhout were kept in closed rooms containing nesting sites. The conditions permitted breeding.

2. Seventy-six experiments, each lasting 6–35 days, were done to test the rats' food preferences. In each experiment except two, a choice was given between two foods, both available in excess. In the two exceptional experiments a choice between three foods was given.

3. Although marked preferences were shown, a food was rarely quite rejected in favour of an alternative.

4. Among cereals, wholemeal was preferred to wheat grains, but wheat grains were preferred to white flour; little or no white flour was eaten if wholemeal was available. Wheat germ was eaten only in small quantities when an alternative cereal was available, but in larger quantities if the alternative was sugar or a sugar-cereal mixture.

5. The addition of sugar or saccharin to cereals increased acceptability; sugar was preferred to saccharin.

6. The addition of arachis oil to wholemeal or wheat increased acceptability.

7. Cod-liver oil at 2·4 % acted as a deterrent.

8. Total calorific intake remained steady over short periods, but over several

weeks rose as the mass of the rat colony increased. The higher the mean weight of the rats in a colony, the lower the calorific intake per unit weight of rat.

9. The amount of food eaten was partly determined by its calorigenic capacity: in particular, wet foods were eaten in much larger quantities than dry foods.

10. The food preferences of wild rats differ in several respects from those of white *Rattus norvegicus*.

11. Apart from palatability or flavour, the main factors influencing food preference were (*a*) previous experience and probably (*b*) the nutritional value of the food. The effect of previous experience was often observed when rats, accustomed to one food, gradually changed from the accustomed food to another. The stages of a change to a new food, or the establishment of a particular preference, varied, and are discussed in detail.

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EXPLANATION OF PLATE 1

Fig. 1. An experimental room: nests and food tray; liver and cabbage have just been put in.

Fig. 2. Food tray: wheat and flour in alternate compartments. (Metal trays of the same design were used in most experiments.)

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