THE BASIC FOOD REQUIREMENTS OF SEVERAL INSECTS

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(With Twelve Text-figures)

It is well known that insects, as a class, feed on an immense variety of different substances, and that each food has its specific insects. But it has never been explained whether, or to what extent, this relationship of insects and food is due to differences in the basic food requirements of different insects. In studying the dietetics of insects it was hoped to find an answer to the question: What determines the distribution of insects on different foods? It was also hoped to gain more information about the requirements of insects for accessory food factors. The advantages in using insects for the identification and estimation of vitamins are obvious and have often been pointed out. The advantage in using for dietary studies insects which normally feed on flour lies in the fact that the diet is powdery and relatively dry. A diet of the consistency of a powder is easy to prepare by mixing ground ingredients together. The normal water content of grain or flour is about 14%. This minimizes the danger of contamination of experimental diets by micro-organisms. The advantages in using insects for the identification and estimation of vitamins are obvious and have often been pointed out. The advantage in using for dietary studies insects which normally feed on flour lies in the fact that the diet is powdery and relatively dry. The ingredients, with the exception of the salts, were mixed in the dry state. The water was added to the salt mixture and the ensuing suspension measured into the diets. MacGollum's salt mixture contains ingredients which are insoluble in water (Ca(H₂PO₄)₂ and Ca-lactate), or which upon adding water form insoluble compounds (Ca++, Fe++, H₂PO₄, SO₄²⁻). Thus it was not possible to ensure exactly the same salt concentration in different diets. The quantity of salts used, 1%, seemed to be ample, and small differences in the salt content of diets seemed of no importance. Only when, in later experiments, yeast was replaced by vitamins in pure substance did the supply of salts apparently become insufficient and the quantity was then doubled.

After adding water plus salts the diets were thoroughly mixed. It is then advisable to leave the diets standing overnight at the temperature and humidity of the experiment and to mix them again. The tests were kept in a room of which the temperature was automatically maintained at 25° C. and the relative humidity at 70%. The water content of diets seemed to undergo no noticeable change during the course of a test. The rate of growth of poikilothermic animals is greatly influenced by change in temperature, and, as we have shown elsewhere for the insects concerned, humidity (Fraenkel & Blewett, 1943 c). To maintain these two conditions constant in a room over long periods was not easy, and slight fluctuations in temperature and relative humidity and occasional breakdowns of the controlling system were unavoidable. Repeats of tests usually, but not always, showed identical results, and in order to eliminate the influence of small fluctuations of temperature and humidity all relevant tests, together with the necessary controls, were performed simultaneously and kept together through the whole experiment. This was particularly important when small differences in the efficiency of different diets were to be demonstrated. Each graph in this and the subsequent papers, with a few exceptions which
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It should be stated, refers to a group of tests performed simultaneously.

It is easy to assess the result of a test if the diet is entirely successful or entirely unsuccessful. In the former case the mortality is low and the rate of growth similar to that on wholemeal flour. In the latter case little or no growth takes place and the larvae die while still small. If a diet is only partly deficient the rate of growth is retarded and the mortality increased. The most significant figure for assessing rate of growth is the duration of larval life until pupation. The methods of assessing results are fully described elsewhere (Fraenkel & Blewett, 1943c). For purposes of summarizing results the following symbols are used:

- + + + + optimum growth resembling wholemeal flour cultures.
- + + + slightly less effective than on wholemeal flour.
- + + still less effective than on wholemeal flour.
- + mortality generally high and development slow.
- ± very unfavourable; development may be completed after long delay by one or two specimens.
- — no specimen completes development.

Most of the results are graphically summarized in curves in which the total number of pupae or adults formed is plotted against time. With an optimal diet growth is fast, the variations between individuals are relatively small, and the mortality is low. The curves therefore are steep and reach a high level. As diets become more unfavourable, growth becomes retarded, the variations between individuals become larger and the mortality rises. The growth curves therefore become shifted to the right, they rise more gradually and only reach a low level. Unfortunately, the curves cannot express the result of totally unfavourable diets when the larvae die before reaching the pupal or adult stage.

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(Figs. 1-5 and Table 1)

The composition of the synthetic diet is described on p. 28. When the carbohydrate used is starch this diet is just as good as wholemeal flour for Tribolium, Silvanus, Sitodrepa and Lasioderma. Ptinus grows on the starch diet very much better than on wholemeal flour. This is probably due to its higher content of B vitamins, supplied in 5% yeast. For Ephestia the synthetic diet was greatly inferior to wholemeal flour.

With glucose substituted for starch the efficiency of the diet remains unaltered for Sitodrepa, while growth of Tribolium, Lasioderma, Silvanus and Ptinus is somewhat retarded. But on other occasions, Tribolium, Lasioderma and Silvanus grew on a glucose diet just as well as on wholemeal flour. Ptinus, on the other hand, always seemed to grow better on starch than glucose. Ephestia grew badly on glucose diets and presented unaccountable difficulties.

The next step in the analysis was to find out whether all the ingredients of the 'complete diet' were essential for the insects tested. Accordingly, carbohydrate, yeast and cholesterol were left out from the diet in separate tests. In the case of yeast and cholesterol which only constitute a small proportion of the diet, the proportions of the remaining substances remained unchanged, which only very slightly alters its percentage composition. In diets without carbohydrates the amount of casein was made up to 100 parts.

When carbohydrates were omitted from the diet,
the rate of growth was generally depressed, which one might have expected of insects living normally on a medium so rich in starch (c. 75%) as flour. There were, however, spectacular quantitative differences. Tribolium, Lasioderma and Ptinus developed noticeably more slowly but still satisfactorily, and the mortality was not increased. Sitodrepa grew very slowly, with only three larvae out of twenty completing development. Silvanus and Ephesia entirely failed to grow without carbohydrates and died as small larvae.

Without cholesterol, both starch and glucose diets became adversely affected but to a very different degree for the different insects. With Silvanus the difference was hardly noticeable; it was slight but definite with Tribolium and Lasioderma. With Ptinus the gap between the efficiency of cholesterol-free and cholesterol-containing diets became still wider.

Sitodrepa grew very slowly without cholesterol and few larvae completed development, while Ephesia entirely failed to grow. From this result it appears that the difference in sterol requirements is less of a qualitative than a quantitative nature, and this will be further analysed below. The cholesterol-free diets contained some ergosterol as a constituent of the yeast in quantity sufficient or almost sufficient for some of the insects and insufficient for others.

Without yeast none of the insects grew and death occurred at an early stage. Fig. 6 shows that the amount of yeast required for optimal growth of Tribolium is probably not very much less than the 5% included in the diets. With 2½% the diet becomes slightly and with smaller amounts increasingly inferior.
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Subsequently the constituent yeast was split into water-soluble and water-insoluble fractions. The water-soluble extract was prepared according to Chick & Roscoe (1930) from fresh brewers' yeast (pitching yeast, supplied by Nicholson’s Brewery, Maidenhead) and was concentrated so that 1 c.c. corresponded roughly to 1 g. of dry yeast. It was used undiluted. ‘Insoluble yeast’ is prepared by boiling fresh brewers' yeast in a large volume of water, filtering and repeating the process nine times. The diet then had the following composition:

- Casein 50
- Cholesterol 1
- Glucose 50
- Yeast extract 15
- McCollum's salt mixture 1
- Insoluble yeast 5

This diet was compared with the original diet which contained yeast instead of the separated soluble and insoluble fractions of yeast, and with diets from which either insoluble yeast alone or in addition cholesterol, was omitted. The results are given in Figs. 7–11 and are summarized in Table 2. It is seen that splitting yeast up into its soluble and insoluble components does not influence the efficiency of the diets. Without insoluble yeast the diet becomes appreciably less efficient. It is shown else-

Silvanus

Fig. 8. *Silvanus surinamensis*. Explanation as Fig. 7.

Lasioderma

Fig. 9. *Lasioderma serricorne*. Explanation as Fig. 7.

Sitodrepa

Fig. 10. *Sitodrepa panicola*. Explanation as Fig. 7.

where (Fraenkel & Blewett, 1943b) that this diet is deficient in an important growth factor, biotin. Leaving out both insoluble yeast and cholesterol, the diet becomes entirely, or almost entirely, inefficient, which demonstrates conclusively the importance of a sterol for all the insects tested. Yeast extract cannot be considered entirely free of ergosterol, and it seems probable that these traces were enough to allow some slow growth of *Tribolium*,

Lasioderma and *Silvanus*. No growth takes place on diets which contain insoluble yeast but no yeast extract.

A diet containing the water-soluble and insoluble fractions of yeast was at first not as efficient as a diet containing whole yeast. The amount of yeast extract used was calculated to correspond to the quantity of yeast from which the extract had been prepared. Since in the original glucose-casein-yeast diet yeast consti-
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tuated about 5%, i.e. 100 mg. in 2 g. of food, the corresponding quantity of yeast extract would be 0.1 c.c., in which 1 c.c. corresponds to 1 g. of dry yeast. Actually 0.15 c.c. was used at first, but on this, with insoluble yeast added, Tribolium grew noticeably slower than on whole yeast. Doubling this quantity of yeast extract restored the efficiency of the yeast extract + insoluble yeast approximately to that of whole yeast. This is shown in Figs. 7-10 where '½ yeast extract' indicates half the quantity of yeast extract which was ultimately used. This is because the yeast and liver preparations were of different strength and it is not obvious on which basis a quantitative comparison should be made. It is, however, clear from the curves of Fig. 12 that liver extract is roughly qualitatively equivalent to yeast extract, and insoluble liver to insoluble yeast.

DISCUSSION

From the results reported in this paper it is clear that all the insects under investigation require cholesterol, and substances contained in the water-soluble and water-insoluble fractions of yeast. They differ, however, in their requirements of carbohydrates. The sterol requirements of the insects in question are further and more fully described and discussed elsewhere (Fraenkel & Blewett, 1943a). Many authors have shown before the need of insects for water-soluble vitamins of the B group (which would be contained in a yeast extract), but the need of insects for a substance contained in the insoluble part of yeast has only very recently been recognized (Fröbich, 1939; Tatum, 1941). A full analysis of the growth factors in yeast, which are required by the insects in question, is given elsewhere (Fraenkel & Blewett, 1943b, d), where it is shown that Tribolium and Ptinus require certainly B1, riboflavin, nicotinic acid, B5, pantothenic acid, choline, and possibly inositol and p-aminobenzoic acid. In addition to these water-soluble factors biotin has been determined as the factor required from insoluble yeast.

The differences with which our insects react to the absence of carbohydrates from the diet requires some comment. While it was to be expected that insects for which flour is a natural food would grow well on a diet which contains large quantities of starch, it has never been investigated whether carbohydrates constitute an essential constituent of the diet of such insects. From the data given in this paper it is clear that some of the insects tested require carbohydrates and others not. From this we would expect the latter group to be able to grow on a much wider variety of natural foods than the former. All the six insects in question are common pests on stored food, and the literature abounds in statements on the occurrence

Table 2. Effect of modifying certain components of the synthetic diet

<table>
<thead>
<tr>
<th>Additions to basal diet</th>
<th>Tribolium</th>
<th>Latioderma</th>
<th>Sitodrepa</th>
<th>Ptinus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yeast</td>
<td>++ +</td>
<td>++ + +</td>
<td>++ +</td>
<td>++ +</td>
</tr>
<tr>
<td>Yeast extract + insoluble yeast</td>
<td>+ + +</td>
<td>+ + + +</td>
<td>++ + +</td>
<td>+ + +</td>
</tr>
<tr>
<td>Yeast extract</td>
<td>+ +</td>
<td>+ + +</td>
<td>+ + + +</td>
<td>++ +</td>
</tr>
<tr>
<td>Yeast extract, no cholesterol</td>
<td>+</td>
<td>+</td>
<td>+ (+)</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 3. Effect of modifying certain components of the synthetic diet

Basal diet: casein 50 parts, glucose 50 parts, salts 1 part, cholesterol 1 part (except last line).

Table 4. Effect of modifying certain components of the synthetic diet

Basal diet: casein 50 parts, glucose 50 parts, salts 1 part, cholesterol 1 part (except last line).

Table 5. Effect of modifying certain components of the synthetic diet

Basal diet: casein 50 parts, glucose 50 parts, salts 1 part, cholesterol 1 part (except last line).

Table 6. Effect of modifying certain components of the synthetic diet

Basal diet: casein 50 parts, glucose 50 parts, salts 1 part, cholesterol 1 part (except last line).

Table 7. Effect of modifying certain components of the synthetic diet

Basal diet: casein 50 parts, glucose 50 parts, salts 1 part, cholesterol 1 part (except last line).
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particular insects on particular foods. While many of these statements must be treated with reserve it is evident that the presence or absence of carbohydrates in the food appears to be one of the decisive factors for the specificity of a food for different insects. Ephesia kuehniella, Sitodrepa and Silvanus, which do not grow without carbohydrates, seem exclusively to infest food with a high carbohydrate content. The occurrence of Ephesia is limited to grain or cereal products like flour, bran, rolled oats and macaroni. Sitodrepa, in addition to these foods, is a pest on dry bread, rusks and biscuits, and Silvanus is known to infest dried fruit which has a very high sugar content. The distribution of the three species which grow in the absence of carbohydrates is very much wider. While occurring in much the same cereal products they also occur on food with a very low carbohydrate content like yeast (Tribolium, Ptinus), tobacco (Lasioderma), fish-meal, dead insects, crude casein, meat-meal (Tribolium, Lasioderma, Ptinus). A full analysis of the nutritional relations

given instead of starch. Glucose was used by us as the carbohydrate in all the vitamin-deficiency tests to be described in the following papers (Fraenkel & Blewett, 1943b-d).

(a) We did not know whether 15-20 % casein would be sufficient for all the insects which we were using or whether casein would optimally satisfy the protein requirements of our insects. To be on the safe side the quantity of casein was increased, and of carbohydrate correspondingly reduced to about 45 % each of the dry diet.

(b) The fact that Tribolium does not require carbohydrates in the diet has been curiously overlooked by other authors. Chiu & McCay (1939), in an attempt to investigate the food value of cane sugar for Tribolium, came to wrong conclusions through failing to recognize that growth is possible without carbohydrate. Tribolium has recently been used by several authors in nutritional experiments, and it is useful to compare the composition of the diets used (Table 3).

The composition of the diets, given by different authors in different units, is expressed in this table in comparable percentages. The figures are only roughly true. These diets differ mainly in the following points:

1. The other authors had starch for the main ingredient of the diet, using it in proportions similar to those in flour. It is well known that starch cannot be obtained in the pure state and that certain vitamin deficiencies only become manifest when sugar is

Table 3. Synthetic diets for Tribolium confusum

<table>
<thead>
<tr>
<th></th>
<th>Frübrich</th>
<th>Offhaus</th>
<th>Chiu &amp; McCay</th>
<th>Barton - Wright</th>
<th>Rosenthal &amp; Reichstein</th>
<th>Fraenkel &amp; Blewett</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>15% casein</td>
<td>1% fresh egg white</td>
<td>20% casein</td>
<td>15% casein</td>
<td>15% casein</td>
<td>45% casein</td>
</tr>
<tr>
<td>Carbohydrate</td>
<td>70% rice starch</td>
<td>76% rice starch</td>
<td>67% maize starch</td>
<td>75% starch</td>
<td>75% rice starch</td>
<td>45% glucose</td>
</tr>
<tr>
<td>Fat</td>
<td>5% cottonseed oil</td>
<td>1% groundnut oil</td>
<td>5% cottonseed oil</td>
<td>3% fat</td>
<td>4% Osborn-Mendel</td>
<td>5% wheat-germ oil</td>
</tr>
<tr>
<td>Cholesterol</td>
<td>5%</td>
<td>5%</td>
<td>5-10%</td>
<td>1-10%</td>
<td>4% Osborn-Mendel</td>
<td>1%</td>
</tr>
<tr>
<td>Yeast</td>
<td>6% Osborn-Mendel</td>
<td>1% Osborn-Mendel</td>
<td>3% Osborn-Mendel</td>
<td>3% Osborn-Mendel</td>
<td>5% McCollum</td>
<td>1%</td>
</tr>
<tr>
<td>Salts</td>
<td>3% K2HPO4</td>
<td>4% Osborn-Mendel</td>
<td>3% Osborn-Mendel</td>
<td>5% McCollum</td>
<td>5% Osborn-Mendel</td>
<td>1%</td>
</tr>
</tbody>
</table>

between stored-product insects and their natural food is given elsewhere (Fraenkel & Blewett, 1943c).

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SUMMARY

1. The method of breeding six different insect species on a 'synthetic' diet consisting of casein, starch or glucose, cholesterol, yeast, salts and water has been described, and the relative importance of the constituents, carbohydrates, sterols and yeast, has been analysed.

2. If the diet contains water-soluble yeast extract instead of whole yeast, it becomes deficient in sterols and another factor contained in the insoluble fraction of yeast.
3. Some of the insects under investigation require carbohydrates and others not. The presence or absence of carbohydrates is shown to be a determining factor in the distribution of insects on different foods.

4. The composition of the 'synthetic' diet is compared with that of similar diets devised for similar purposes by other authors.

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REFERENCES


