

Nutrition and Diet of Muscoid Flies

D. SPILLER¹

The muscoid flies are a segment of that large ecological group, the filth flies. These are attracted to decomposing organic matter for feeding or depositing their eggs or larvae. Sometimes the adults have such marked preferences that breeding is largely confined to a single material, e.g., *Musca sorbens* which oviposits on human faeces (Hafez & Attia, 1958). Some, such as the common housefly, are less selective and oviposit on a wide range of materials from poultry droppings to lawn clippings. There is no real evidence that this ecological selectivity is linked with essential nutritional requirements and in the laboratory many of the muscoid flies, and indeed filth flies, can be reared on similar media (Snyder, quoted by Peterson, 1953).

ADULT NUTRITION REQUIREMENTS

The nutritional requirements of adults present no difficulties in laboratory culture. Life can be sustained adequately on glucose and some other monosaccharides and water (Greenberg, 1959). Exogenous protein (or amino-acids) is usually required for egg development (Ascher & Levinson, 1956); milk is commonly used. Autogeny is possible but exceptional (Robbins & Shortino, 1962). Vitamin requirements are probably met partly by autolysis of intestinal bacteria, partly by carry-over from the larval stage; neither B-vitamins nor a mixed bacterial "chow" improved longevity of sterile adults (Greenberg & Burkman, 1963). Additional cholesterol improves egg hatching (Monroe, 1960).

LARVAL NUTRITION REQUIREMENTS

It is not known which portions of the natural diets are utilized by larvae, but obviously much of the feeding is on products of bacterial decomposition and on bacteria themselves (Levinson, 1960) and neither is suitable for defining nutritional require-

ments. These needs have been determined on sterile or partially simplified diets; only *M. domestica* and *M. d. vicina* have been investigated.

Carbohydrate

Larvae neither require carbohydrate nor markedly benefit if it is supplied; moderate amounts of glucose, starch or glycogen are tolerated and appear marginally beneficial. Fructose, sucrose, ribose and raffinose inhibit growth; lactose has not been tested (Brookes & Frankel, 1958).

Fats

There is no obvious requirement for fats, fat-soluble factors or fatty acids (Brookes & Frankel, 1958). Some are toxic or inhibitory (Levinson & Ascher, 1954).

Proteins

The essential amino-acids are probably the same as for other animals; tryptophan is certainly essential (Chang & Wang, 1958). The "biological value" of different proteins is unknown.

Vitamins

M. domestica has confirmed larval requirements for six vitamins, thiamine, riboflavine, pyridoxine, nicotinic acid, pantothenic acid and biotin (Brookes & Frankel, 1958; House & Barlow, 1958). A further vitamin, folic acid, is required if the diet is deficient in purine or pyrimidines (Brookes & Frankel, 1958). A need for choline has been reported (House & Barlow, 1958) but not confirmed (Brookes & Frankel, 1958).

Sterols

As far as is yet known all insects require, but cannot synthesize, sterols (Gilmour, 1961). Hence sterols are an essential part of the diet of all insects although in some these requirements are provided by intestinal or intracellular organisms. In all cases the sterol demand can be met by cholesterol or dehydrocholesterol. All insects except dermestids can use the plant sterols stigmaterol and sitosterol and the

¹ Senior Principal Scientific Officer, Plant Diseases Division, Department of Scientific and Industrial Research, Auckland, New Zealand.

yeast sterol ergosterol. *Musca* is one of the few insect genera that cannot use the saturated derivative cholesterol but otherwise its sterol requirements are not unusual.

The function of sterols in muscoid nutrition is uncertain. Protein synthesis or transport appears to be involved either directly or indirectly. On some milk-yeast diets addition of cholesterol has improved numbers reared and adult weights (Hammen, 1957; Arevad, 1963); in another case pupal numbers and weight, initial and total eggs production were unaffected (Spiller, 1963). When the CSMA¹ larval medium was supplemented with 1% cholesterol about half the reared flies developed mature ovaries and laid viable eggs when fed sugar and water alone; sitosterol was ineffective (Robbins & Shortino, 1962).

Water

The strictly nutritional requirements are probably small and easily met from the large amounts required in a successful medium.

Mineral

The inorganic requirements have not been determined.

STERILE DIETS

Sterile diets have been prepared. On most synthetic sterile diets growth is slower and adults are smaller than on practical diets (Brookes & Frankel, 1958; Chang & Wang, 1958; House & Barlow, 1958). Possibly this is due to excess water or inadequate ventilation in the sterile diets, for similar effects have been noted on agar-based practical diets (Arevad, 1963). It could also be a temperature effect. Rather small numbers of larvae are used for sterile rearing, hence there is less metabolic heat, which may increase standard mass cultures as much as 12° C above ambient temperature. It may be significant that a high rearing temperature was used in the one sterile rearing technique reported to equal the CSMA diet (Monroe, 1962).

MICRO-ORGANISMS

Larvae feed in nature on media rich in micro-organisms. In nature and in practical diets micro-organisms probably provide adequate vitamins and additional sterol but if these are otherwise present

micro-organisms are neither essential nor beneficial (Chang & Wang, 1958). In most diets the micro-organisms are those adventitious in the ingredients. These micro-organisms develop rapidly in wet medium but it is a matter of chance which becomes dominant. In my laboratory the initial count of the milk-yeast-paper medium is about 5×10^8 and rises in four days to 5×10^{10} . About five bacteria are abundant, of which one is strongly proteolytic and when dominant, causes unpleasant odours. In some rearing media the freshly-mixed ingredients are regularly seeded with known micro-organisms. This is standard with CSMA medium where the micro-organism is yeast and it has been done effectively for *M. d. vicina* where the bran-based medium is seeded with a mixture of *Escherichia coli*, *Sarcina* and *Lactobacillus* (Silverman & Silverman, 1953). Such deliberate seeding is a worth-while step towards increasing the uniformity of cultures and is now being attempted for the yeast-milk-paper medium in my laboratory.

PRACTICAL DIETS

Practical diets, which are not sterile, cannot be fully defined. The major criteria are the practical requirements that it should be possible to rear a steady supply of relatively uniform flies and that the diet should be clean, easy to prepare, and not too costly. Early attempts at laboratory culture of muscoid colonies used natural media; sometimes cow dung (Feldman-Muhsam, 1944), or pig dung (Hafez, 1949, quoting Lörincz & Makara, 1935), or pig dung and horse manure (Hockenyos, 1931), or, most often, horse manure (Glaser, 1924; Grady, 1928).

It was found that houseflies could not be reared on horse manure in winter in New York and Pennsylvania although other conditions were considered suitable (Glaser, 1927; Grady, 1928). When dead yeast was added in abundance houseflies were reared throughout the year (Glaser, 1927). These natural or modified natural diets were unsatisfactory, firstly because of uncertain availability and secondly because of frequent accidental introduction of parasites into fly cultures (Richardson, 1932). To eliminate parasites the horse manure could be pasteurized at 70° C for two hours without reducing its value (Peterson, 1953). If this was not done, a mite parasitic on flies was often brought in and, once established, proved difficult to eliminate from the fly colony (Richardson, 1932).

¹ Chemical Specialties Manufacturers' Association.

These difficulties led first to Richardson's medium, containing wheat bran, alfalfa meal, yeast and malt (Richardson, 1932), and then to the CSMA medium which contains in addition spent brewers' grains (Soap Blue Book, 1956). There is also a very simple, bran, straw, and bacteria mix, which is used to rear *M. d. vicina* (Silverman & Silverman, 1953). Generically this group of media can be regarded as artificial horse manures and is characterized by being entirely vegetable in origin. As the vegetable constituents, the yeasts and other micro-organisms supply the whole diet, the sterols available will in general be phytosterols not zoosterols.¹ Very large numbers of flies have been, and are being, reared on these diets but the diets have inherent disadvantages. Bran, alfalfa and grain are such complex and variable natural products that they are difficult to standardize and, further, there is not much prospect of simplifying and modifying the ingredients leading on to the defined standard diets which are desirable.

The other group of practical diets utilizes mainly animal protein, usually supplemented with yeast and a variable bacterial flora. Sterile culture has been accomplished on swine-liver coagulum and yeast (Glaser, 1938) and in some laboratories houseflies are reared on ground horsemeat (Hammen, 1957). Diets based on milk and milk products are now gaining in acceptance and recent improvements (Spiller, 1963) in ease of preparation should accelerate this trend.

In the simplest milk diets larvae are reared on pads of cotton-wool or absorbent tissue soaked with milk (Hafez, 1949; Fisher & Morrison, 1949). However, most milk diets are now based on dried

milk powders and contain dried yeast. For adequate rearing these diets must contain rather large amounts of water. To prevent this forming an unusable mush, the water is supported either with an agar gel or with paper. The paper may be either mashed with the mix (Fisher & Jursic, 1958) or, as in my recent modification, ground to a flock and then added (Spiller, 1963).

Recent tests indicate that agar-based diets give small pupae (Arevad, 1963). On my medium of whole dried milk 60 g, yeast 6 g, water 270 ml, flocked paper 60 g, pupae weighing 20-21 mg can be obtained if the amount of eggs does not exceed 0.4 ml. On the usual seeding of 0.8 ml the pupae weigh 16-18 mg; with increased egg volume the pupal size is greatly reduced but the bio-mass becomes constant, and up to 5000 pupae have been reared on one mix.

The initial proportions of the ingredients in this medium were taken fairly arbitrarily but current attempts to improve the medium have failed. This brings me to the final and perhaps most important point regarding muscoid nutrition and insect culture generally. Provided the basic nutritional requirements are met and provided the physical form of the medium is acceptable, there is probably no such thing as *an* optimum diet. This is because alterations in the proportion of one component demand simultaneous alterations in the proportions of other ingredients (Sang, 1959), if optimum conditions are to be maintained. Hence there is a multiplicity of diets, all equally "optimum" (Sang, 1959). Perhaps the commonest mistake is to assume that the optimum diet for one colony of a particular species will be the same as for another colony. This is to forget that laboratory populations are continuously exposed to natural selection for maximum fitness on the medium supplied. After a number of generations the strain being reared will have maximized its fitness in relation to the diet, and any major alteration will then be sub-optimal for that particular strain.

¹ Cholesterol has recently (Johnson, Bennett & Hofman, 1963) been isolated from two higher plants, the potato and the yam, thus invalidating the absolute distinction between phytosterols from plants and zoosterols from animals. The importance to insect, and hence muscoid, nutrition is that entirely vegetable diets can no longer be assumed to be cholesterol-free.

REFERENCES

- Arevad, K. (1963) In: *Annual Report of the Government Pest Infestation Laboratory, 1959-1960*, Springforbi, Denmark, pp. 53-54
- Ascher, K. R. S. & Levinson, Z. H. (1956) *Riv. Parasit.*, **17**, 217
- Brookes, F. J. & Frankel, G. (1958) *Physiol. Zool.*, **31**, 208
- Chang, J. T. & Wang, M. Y. (1958) *Nature (Lond.)*, **181**, 566
- Feldman-Musham, B. (1944) *Bull. ent. Res.*, **35**, 53
- Fisher, R. S. & Morrison, F. O. (1949) In: *Annual Report of the Entomological Society of Ontario*, vol. 80, pp. 41-45

- Fisher, R. W. & Jursic, F. (1958) *Can. Ent.*, **90**, 1
- Gilmour, D. (1961) *The biochemistry of insects*, New York & London, Academic Press
- Glaser, R. W. (1924) *J. econ. Ent.*, **17**, 486
- Glaser, R. W. (1927) *J. econ. Ent.*, **20**, 432
- Glaser, R. W. (1938) *J. Parasit.*, **24**, 177
- Grady, A. G. (1928) *J. econ. Ent.*, **21**, 598
- Greenberg, B. (1959) *J. cell. comp. Physiol.*, **53**, 169
- Greenberg, B. & Burkman, M. (1963) *J. cell. comp. Physiol.*, **62**, 17
- Hafez, M. (1949) *Bull. ent. Res.*, **39**, 385
- Hafez, M. & Attia, M. A. (1958) *Bull. Soc. ent. Egypte*, **42**, 83
- Hammen, C. S. (1957) *Ann. ent. Soc. Amer.*, **50**, 125
- Hockenyos, G. L. (1931) *J. econ. Ent.*, **24**, 717
- House, H. L. & Barlow, J. S. (1958) *Ann. ent. Soc. Amer.*, **51**, 299
- Johnson, D. F., Bennett, R. D. & Hoftman, E. (1963) *Science*, **140**, 198
- Levinson, Z. H. (1960) *Nature (Lond.)*, **188**, 427
- Levinson, Z. H. & Ascher, K. R. S. (1954) *Riv. Parasit.*, **15**, 111
- Monroe, R. E. (1960) *Ann. ent. Soc. Amer.*, **53**, 821
- Monroe, R. E. (1962) *Ann. ent. Soc. Amer.*, **55**, 140
- Peterson, A. (1953) *A manual of entomological techniques*, Ann Arbor, Mich., Edwards Bros Inc.
- Richardson, H. H. (1932) *Science*, **76**, 350
- Robbins, W. E. & Shortino, T. J. (1962) *Nature (Lond.)*, **194**, 502
- Sang, J. H. (1959) *Ann. N.Y. Acad. Sci.*, **77**, 352
- Silverman, P. H. & Silverman, L. (1953) *Riv. Parasit.*, **14**, 89
- Soap and Chemical Specialties Blue Book*, 1956, New York, MacNair-Dorland, pp. 243-244
- Spiller, D. (1963) *Nature (Lond.)*, **199**, 405