

# METABOLISM OF NUTRIENTS IN THE ADULT MOSQUITO<sup>1</sup>

EMILE VAN HANDEL

Florida Medical Entomology Laboratory, University of Florida—Institute of Food and Agricultural Sciences, 200 9th Street S.E., Vero Beach, FL 32962

**ABSTRACT.** The metabolism of dietary carbohydrates (nectar) and proteins (blood) explains many aspects of the behavior of adult mosquitoes. The energy flow of the reserve carbohydrates (glycogen) and fat (triglycerides) was followed at rest, in flight, and at different temperatures. A main characteristic of female mosquitoes is the accumulation of large amounts of fat from sugar meals, and the use of these reserves for survival at rest, but not for vigorous flight activity. Whether dietary sugar will be stored as glycogen (that is available for flight) or as fat, is regulated by neurosecretory cells of the brain. While sugar is used entirely for energetic purposes, a large blood meal may also contribute some nutrients for glycogen and fat accumulation.

## INTRODUCTION

Unlike larvae that feed indiscriminately on solutes and particles in their aquatic habitat, adult mosquitoes have highly specialized feeding habits. Their energy requirements are met in 3 distinct ways. They may depend on reserves already present at emergence, or they may acquire a blood meal from a vertebrate host or a sugar meal from plants. Energy reserves accumulated during the feeding stage of the last larval instar, although diminished during the non-feeding pupal stage, are usually sufficient to maintain the adults for several days.

During the past 2 decades, development of new or modified chemical methodology has made it possible to follow the appearance and disappearance of energy reserves in individual mosquitoes. The purpose of the present article is to use the changes that take place inside the mosquito for the interpretation of mosquito behavior. It may be useful to review and interpret earlier results that may be relevant to the ecology and control of adult mosquitoes. The emphasis is on work done in my laboratory with the Florida salt marsh mosquitoes. No attempt has been made to cover the complete literature.

The way in which the female metabolizes sugar and blood affects its longevity, flight range and vectorial capacity. In contrast to the male mosquito, the female supported by stored fat can survive a long time, resting on the ground or under dense foliage, in spite of unfavorable nutritional and climatic conditions. This may be one of the reasons that adulticiding populations seems to afford only short-term relief. Not in need of an immediate food source, be it blood or nectar, females may survive to bite another day.

food of male mosquitoes and of species not known to suck blood. There are numerous observations of mosquitoes visiting flower heads, but reliable evidence that the crop contains nectar sugars is scarce.

The sugar meal sustains the female mosquito until it finds its host and allows an infected mosquito to live long enough to oviposit, to bite repeatedly, and to become infective. Feeding on floral and extrafloral nectar, fruits and other plant juices therefore plays an important, indirect role in disease transmission. A systematic survey of nectar feeding by mosquitoes collected from the field became more practical after the development of a simple test that made it possible to detect nectar in an intact mosquito. A single reagent (cold anthrone) reacts specifically with fructose (Van Handel 1967a) and not with glucose. Glucose is produced by the mosquito itself, is ingested with each blood meal, and rapidly accumulates after the insect's death by breakdown of stored carbohydrates. Fructose and sucrose are specific for nectars and fruit juices, and therefore, can be used as "markers." This was confirmed by the analysis of a large number of flower nectars and fruit juices (Van Handel et al. 1972). Cold anthrone reagent splits sucrose into glucose and fructose and produces a green-blue color with the latter. It is possible to test hundreds of individual mosquitoes within a few hours for the presence of nectar without the tedium of dissecting the crop (Van Handel 1972a). A negative anthrone test does not mean that the mosquito has never fed on nectar. If the sugar is absorbed, it is converted to products that do not react (trehalose, glycogen, fat, carbon dioxide) so that the percentage of the population that has fed is always higher than the test indicates.

Using the new test, Bidlingmayer and Hem

## NECTAR AS A SOURCE OF FOOD

It is assumed that in nature, plant juices, particularly flowers (nectar), form the principal

<sup>1</sup> Institute of Food and Agricultural Sciences, University of Florida Experiment Station Journal Series No. 5599.

(1973) surveyed 24 species, collected both by power aspirator and suction traps, and after analysis of several thousands of mosquitoes, established the frequency of nectar feeding for both sexes. The largest percentage of individual mosquitoes containing nectar was found in *Ae. taeniorhynchus* (Wied.), followed by *Culex nigripalpus* (Theobald). The percentage was much lower in *Uranotaenia* species, a group not known to feed on warm blooded animals. Several more recent studies have depended on the cold anthrone test, not only for mosquitoes (Magnarelli 1978, 1979, 1980, 1983) but also for Tabanidae (Magnarelli and Anderson 1981) and *Culicoides* (Magnarelli 1981).

#### THE DETERMINATION OF CALORIC RESERVES

All long-range activities of mosquitoes are dependent on available caloric reserves. A knowledge of these reserves would allow predictions on the minimal time a brood can survive when it does not take additional meals. Simple methods are available for this purpose. When mosquitoes are maintained on water at a constant temperature, the time to reach 50% mortality becomes an accurate measure of biologically available reserves, irrespective of the nature of these reserves (Van Handel 1972b; Fig. 1). After eclosion, when female *Ae. sollicitans* (Walker) were fed on 10% sugar solution for a week, then maintained on water only, 50% of the population died in 37 days at 15°C and in 21 days at 22°C from the time the sugar was removed. When mosquitoes are caught in

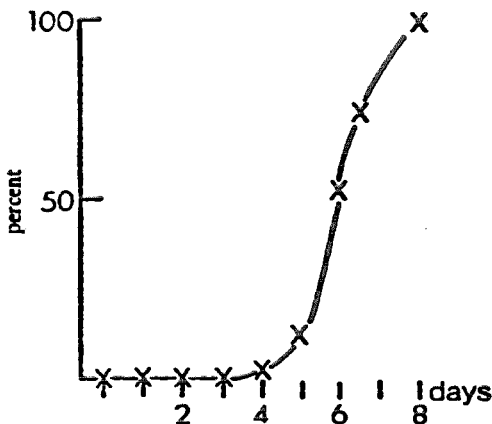


Fig. 1. Cumulative mortality of *Aedes sollicitans* maintained from emergence at 25°C on water (Van Handel 1972b).

the field and maintained in the laboratory at a constant temperature on water only, their survival time is proportional to the caloric reserves at the time of capture.

An alternative to the above biological analysis of caloric reserves is the complete oxidation to carbon dioxide of the entire mosquito with an acid solution of bichromate (Van Handel 1972b). This reagent oxidizes the entire mosquito, including protein, lipids, carbohydrates and chitin to  $\text{CO}_2$ , while reducing the red  $\text{Cr}^{\text{VI}}$  to the green  $\text{Cr}^{\text{III}}$  ion. When a population is brought in from the field, it can be split into two groups. One group is assayed immediately, and a control group is starved to death and then assayed. The difference in the bichromate value of these two groups represents the available caloric reserves. This is illustrated for *Ae. sollicitans* starving or feeding from the day of emergence (Fig. 2). This method is not valid for blooded or gravid females, since a large portion of the blood meal is used for production of eggs, and the eggs are not available caloric reserves.

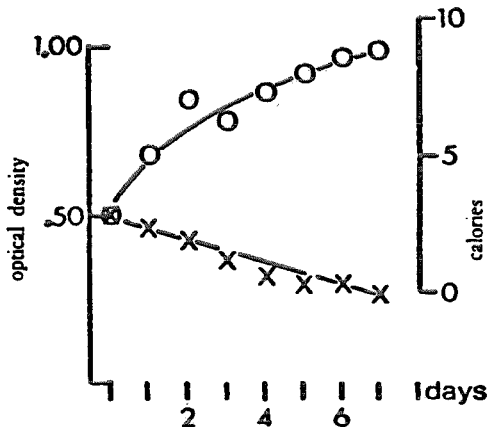


Fig. 2. Bichromate values of *Aedes sollicitans* starving (-x-x-) or feeding (-o-o-) from emergence (Van Handel 1972b).

The caloric reserves of the mosquito are synthesized in the so-called "fat body," which is a group of cells attached to the wall of the abdomen. This organ is not equivalent to the vertebrate fat cells (adipose tissue), but more to the vertebrate liver. The fat body synthesizes the hemolymph sugar trehalose and the yolk that will be stored in the developing eggs. In addition, it synthesizes and stores carbohydrate (glycogen) and fat (triglycerides).

## DEPENDENCE OF LONGEVITY ON TEMPERATURE

At adult eclosion, mosquitoes carry over nutritional reserves from the pupal stage. They can survive for some time in the field, devoid of any available source of sugar. It can easily be determined how long these reserves will last by letting pupae, collected in the field, emerge in the laboratory. Then the mortality can be recorded as a function of time. The lower the temperature, the longer the energy reserves will last. This was investigated (Fig. 3) in *Ae. sollicitans* starved from emergence (Van Handel 1973). The data are presented as an Arrhenius plot: the logarithm of time, at which 50% of the population had died, or used 50% of its energy, lies on a straight line when plotted against the reciprocal of absolute temperature (Fig. 3). When the temperature rises (or drops) 10°C, use of energy and mortality increase (or decrease) between 2.1 and 2.3 times. Live mosquitoes, being cold-blooded, follow the same natural law that has been established for most chemical and biochemical reactions. This result has practical value. When the caloric reserves from a trapped sample population is determined, and the temperature patterns in the field are known, the minimum longevity of the brood can be predicted. This is important at low temperatures, when flight activity is inhibited and flowers are not abundant. Of course, when they are able to take additional food, the life expectancy is extended. Most Florida mosquitoes become immobile when the temperature drops below 15°C, but are not in true diapause. Diapause would cause a clear break in the Arrhenius plot, and they would not increase mobility and energy utilization by an increase in temperature. This may be different in northern species, known to overwinter as adults. However, it has not been firmly established whether

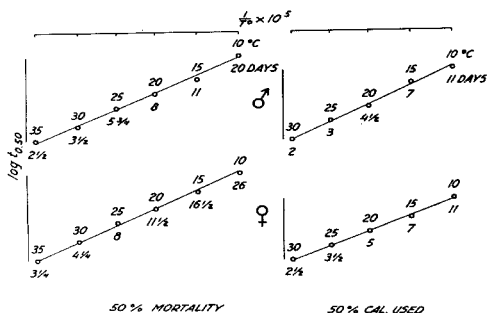


Fig. 3. Mortality and utilization of energy by *Aedes sollicitans* starved from emergence.

these mosquitoes are in diapause, or only immobilized by low temperatures.

## SEXUAL DIFFERENCES IN FAT STORAGE

At adult eclosion, male and female mosquitoes contain small amounts of fat. When maintained on sugar, the fat content of the female rises steadily; whereas during the same time, fat nearly disappears from the male. When larvae of an "intersex" strain of *Ae. aegypti* (Linn.) were raised at 33°C, both external and internal dimorphic characters of the males were feminized. Yet, these feminized males were unable to accumulate fat, and metabolically, remained males (O'Meara and Van Handel 1971). In *Ae. sollicitans* maintained on sugar, within a few days of eclosion, the fat content of the female was 50 times that of the male (Van Handel and Lum 1961). This sexual difference seems to be unique to mosquitoes. House flies consume the residual fat from the pupal stage without the ability to replenish it in either sex (Fig. 4). Even when these flies are maintained on a fat-free source of protein, the pupal fat disappears. The blood-sucking fly *Stomoxys calcitrans* maintained on sugar, behaves similarly: neither sex accumulates appreciable amounts of fat (unpublished results). These flies and the male mosquito require a readily available food source. Well-fed female mosquitoes survive a long time without food (Fig. 5).

If the female mosquito is starved until no fat remains, and then fed on sugar, newly synthesized fat appears that is known to be made entirely from sugar. This fat has been isolated and studied under a variety of physiological conditions. These studies answered a question that had long eluded cell biologists who used either warm-blooded animals or microorganisms in their experiments: namely, can the same cell make a harder (more saturated) fat at higher and a more liquid (unsaturated) fat at lower temperatures? The starved mosquito, fed on sugar and then held at temperatures from 5 to 30°C, always synthesized exactly the same type of fat, specific for the species, not for the temperature at which the synthesis took place. The mosquito can make only one type of fat, the type for which it is genetically programmed (Van Handel 1966). This conclusion is presumably valid not only for the mosquito, but for all other animals, and since its publication, has never been challenged. Fat more suitable to cold conditions would enhance the female's ability to overwinter in cold climates. Even *Culex pipiens* (Linn.) raised from eggs collected in Ontario, did not change its fat composition

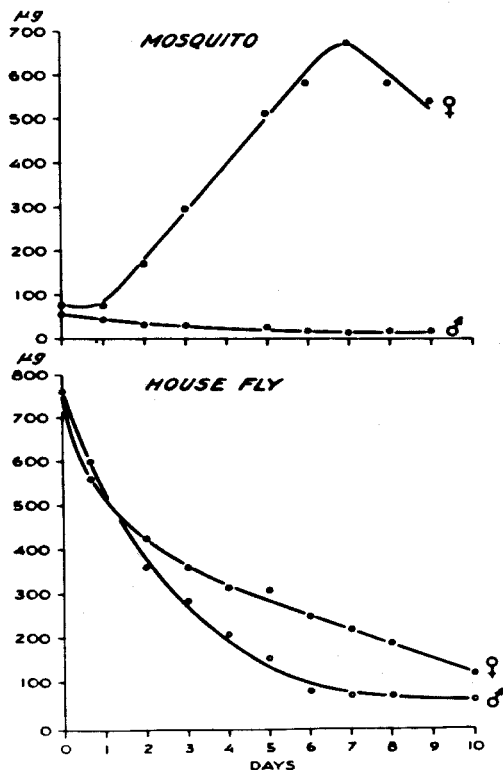


Fig. 4. Triglyceride levels of *Aedes sollicitans* and *Musca domestica* maintained on sugar after emergence (Van Handel and Lum 1961).

under the pressure of low temperature and short photoperiod (Van Handel 1967b).

#### THE METABOLIC FATE OF A SINGLE SUGAR MEAL

We analyzed a large number of fruit juices and flower nectars and found that more than 95% of the sugars consisted of a mixture of glucose, fructose and sucrose (Van Handel et al. 1972). More complex sugars were absent or present in traces only. Reports in the literature that sorbitol, a sugar alcohol, is sometimes present in significant amounts, were not confirmed. Mosquitoes can live on a solution of sorbitol for as long as on a solution of glucose, fructose or sucrose (Galun and Fraenkel 1957), and therefore, mosquitoes must have a pathway to use this alcohol effectively.

Foraging mosquitoes will completely engorge

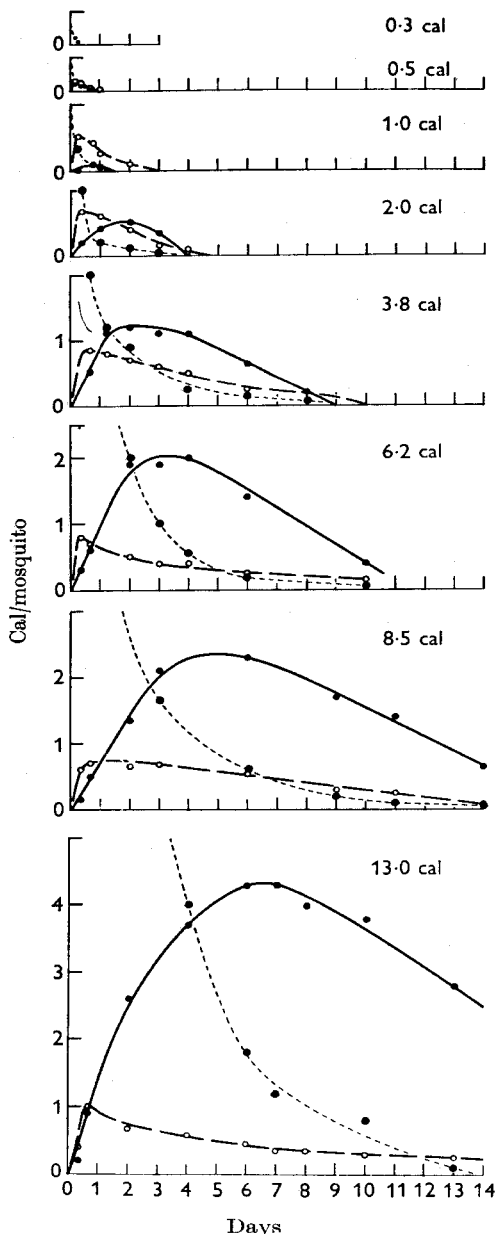


Fig. 5. The appearance and disappearance of carbohydrate and fat in *Aedes sollicitans*, fed on single doses of 0.3–13 cal (0.075–3.3 mg) sugar. Filled circles, full lines, triglycerides; empty circles, glycogen; filled circles, interrupted lines, sugar.

on nectar or, more likely, take multiple meals over a short time span, e.g., during peak flight activity. Metabolically, this is equivalent to a single sugar meal of variable sugar content. Female *Ae. sollicitans* were starved for a few days after emergence, fed individually from a micropipette on sugar solutions, and then maintained at 27°C with access to water only. The sugar meals ranged from 0.075 to 3.3 mg per female. In order to make the energy provided by fat comparable to that of sugar and glycogen (or protein), the values were expressed as calories per mosquito, instead of mg (1 mg fat = 9 cal; 1 mg sugar, glycogen or protein = 4 cal).

When *Ae. sollicitans* was fed 0.3 cal (0.08 mg) of sugar, neither glycogen nor fat was deposited; all sugar was used to provide energy. Meals between 0.5 and 1 cal result in increasing glycogen accumulation until a plateau is reached. Sugar beyond 1 cal does not increase glycogen levels, but induces fat deposition. After ingesting 2 cal (0.5 mg) of sugar, fat reaches almost the same level as glycogen; after 4 cal (1 mg) of sugar, fat surpasses the glycogen plateau and ever increasing sugar meals are reflected in ever increasing amounts of fat (Van Handel 1965, Fig. 5).

As in many other insects, the main hemolymph sugar of the mosquito is the disaccharide trehalose, not the monosaccharide glucose. When glucose is absorbed from the gut, it is converted by the fat body to trehalose that is secreted into the hemolymph and to glycogen that is stored. This conversion takes place through a number of intermediate steps, starting with production of glucose phosphate (Van Handel 1969a). The pathway in the mosquito appeared not to be different from that already known in locusts and moths (Candy and Kilby 1961, Murphy and Wyatt 1965). More interesting is the way in which the mosquito metabolizes fructose. Before fructose can be converted to trehalose and glycogen, it must form a phosphate, as does glucose. But, there is another reaction that does not require phosphorylation. The fat body contains an enzyme (polyol:NAD oxidoreductase) that rapidly reduces fructose to the polyalcohol sorbitol, and just as rapidly can oxidize sorbitol back to fructose. When one injects either fructose or sorbitol into the hemolymph, it always contains a mixture of both (Van Handel 1969b). This explains why mosquitoes survive on sorbitol as long as on fructose or glucose.

### THE FUEL FOR LONG FLIGHTS

Lepidoptera (Van Handel 1975), locusts and migrating birds largely or entirely depend on stored fat to provide energy for sustained

flight. To study the type and amount of fuel used by mosquitoes, we have used an enclosed flight mill which allowed us to record the distance flown and to trap the respired carbon dioxide for analysis. In both sexes of *Ae. taeniorhynchus* and *Ae. sollicitans*, flight was sustained by the utilization of carbohydrate (glycogen in unfed, sugar in fed mosquitoes). Energy consumption during flight was 4 times greater than in non-flown controls (Nayar and Van Handel 1971). There are notable differences between mosquitoes in free flight and mosquitoes forced to fly to exhaustion on a flight mill. However, the main conclusion that both sexes of mosquitoes fly on carbohydrates and not on fat, will remain valid.

Feeding on nectar provides immediate flight energy, but prolonged rest after the meal would lead to the accumulation of fat, which can not be used for flight. If the exhausted mosquito acquires a blood meal instead of nectar, at least a day is required before enough glycogen is synthesized from blood protein to resume flight (Nayar and Van Handel 1971). Furthermore, most of the blood proteins are used for egg development, and this limits the nutrients available to accumulate glycogen as a fuel for flight.

### DIGESTION AND METABOLISM OF THE BLOOD MEAL

Blood ingested by a mosquito is directed to the posterior midgut which is capable of considerable expansion. After the meal, a peritrophic membrane begins to form around the blood clot. In *Cx. nigripalpus*, formation begins immediately, but completion takes at least 12 hours (Romoser and Cody 1975). When fully formed, the peritrophic membrane separates the blood meal from direct contact with the gut wall. In *Ae. aegypti*, most of the enzyme activity needed to digest the blood is found between the midgut epithelium and the membrane, and very little in the blood bolus itself. Presumably, digestion of blood takes place in the narrow compartment between gut wall and peritrophic membrane (Graf and Briegel 1982). Vertebrate blood contains powerful inhibitors of trypsin, the main enzyme associated with digestion of blood in *Ae. aegypti* (Huang 1971). If the membrane were not formed, the anti-trypsins in the blood bolus would inactivate the trypsin secreted by the mosquito gut. Whether the peritrophic membrane is indeed essential for the digestion of the blood meal, still lacks reliable experimental evidence.

The digestion products of the blood (mostly amino acids) are absorbed through the gut wall into the hemolymph and transformed by the fat

body into other products, the most important of which is the protein vitellogenin that is absorbed by the ovary and laid down as yolk. How the blood initiates the synthesis of vitellogenin in mosquitoes has been actively investigated over the past decade, but no consensus has been reached (reviewed by Fuchs and Kang 1981).

Once fertilized eggs are laid, the yolk is used as food for the embryos. Since yolk has little or no nutritional value for the gravid female, I will not review the extensive literature on egg development. Many mosquitoes, including *Ae. taeniorhynchus* and *Ae. sollicitans*, take blood meals that are usually larger than needed to mature an egg batch. The excess is used to accumulate fat and glycogen (Van Handel 1965). It is difficult to estimate what portion of the blood meal is used for egg development and how much for nutritional purposes. In order to compare the nutritional value of blood with that of sugar, we have surgically removed the ovaries before the meal. When these mosquitoes were fed an equicaloric meal of either sugar or blood, there was no difference in either the amount of glycogen or the amount of fat that was synthesized (Fig. 6).

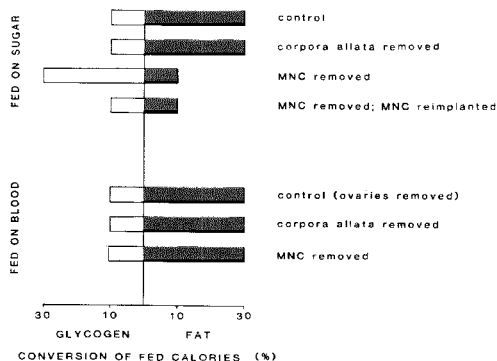


Fig. 6. Endocrine regulation of glycogen and fat synthesis in *Aedes taeniorhynchus*. Females were starved, then fed 4 cal of either sugar or protein (blood), and analyzed one day later. MNC = medial neurosecretory cells of the brain.

When the blood is digested, the end product of amino acid metabolism is excreted as ammonium urate (Van Handel 1975), a colorless, soluble crystal. The black spots excreted by blood-fed mosquitoes consist of heme, an iron-containing breakdown product of hemoglobin, the red pigment of blood cells.

## THE ENDOCRINE CONTROL OF FAT AND GLYCOGEN ACCUMULATION

When *Ae. sollicitans* and *Ae. taeniorhynchus* were fed a single dose of sugar, a small amount of glycogen and a large amount of fat was deposited 24 hr later. However, when the medial neurosecretory cells of the brain (MNC) were surgically removed before the meal, the opposite occurred: a large amount of glycogen and a small amount of fat accumulated (Van Handel and Lea 1965).

Reimplantation of MNC in *Ae. taeniorhynchus* from which the MNC were first removed reduced the glycogen storage capacity to the low level of intact controls, but did not restore the ability to make and store more fat (Lea and Van Handel 1970). This control of fat and glycogen synthesis applies to sugar-fed females only. In blood-fed females removal of MNC had no effect on glycogen and fat storage (Van Handel and Lea 1970). The corpora allata, glands that produce the juvenile hormones, have no effect on glycogen and fat storage of either sugar-fed or blood-fed females (Van Handel and Lea 1970). A summary of all findings is presented in Fig. 6.

Behavioral information stored in the mosquito's brain cells is bewilderingly complex and not as accessible and well studied as comparable information in vertebrates. Hormonal signals that regulate behavior are continually exchanged between the MNC, the corpora allata, the ovaries and the fat body cells. It is not always easy to establish whether these hormones regulate metabolic or reproductive activities, or whether the same endocrine glands produce hormones with different chemical composition and function. However, we have firmly established that neurosecretory cells of the brain (MNC) regulate whether the sugar meal will be used for the accumulation of fat or of carbohydrate. This in turn determines many aspects of mosquito behavior such as type and duration of flight, survival and mating.

## ACKNOWLEDGMENTS

I thank the personnel of several Florida Mosquito Control Districts and the Office of Entomology for critical remarks. The author's work was supported by grants from the National Institutes of Health.

## References Cited

- Bidlingmayer, W. L. and D. G. Hem. 1973. Sugar feeding by Florida mosquitoes. *Mosq. News* 33:535-538.

- Candy, D. J. and B. A. Kilby. 1961. The biosynthesis of trehalose in the locust fat body. *Biochem. J.* 78:531-536.
- Fuchs, M. S. and S. H. Kang. 1981. Ecdysone and mosquito vitellogenesis: A critical appraisal. *Insect Biochem.* 11:627-633.
- Galun, R. and G. Fraenkel. 1957. Physiological effects of carbohydrates in the nutrition of the mosquito *Aedes aegypti* and two flies *Sarcophaga bullata* and *Musca domestica*. *J. Cell Comp. Physiol.* 50:1-23.
- Graf, R. and H. Briegel. 1982. Comparison between aminopeptidase and trypsin activity in blood-fed females of *Aedes aegypti*. *Rev. Suisse Zool.* 89:845-850.
- Huang, C. T. 1971. Vertebrate serum inhibitors of *Aedes aegypti* trypsin. *Insect Biochem.* 1:27-38.
- Lea, A. O. and E. Van Handel. 1970. Suppression of glycogen synthesis in the mosquito by a hormone from the medial neurosecretory cells. *J. Insect Physiol.* 16:319-321.
- Magnarelli, L. A. 1978. Nectar-feeding by female mosquitoes and its relation to follicular development and parity. *J. Med. Entomol.* 14:527-530.
- Magnarelli, L. A. 1979. Diurnal nectar-feeding of *Aedes cantator* and *A. sollicitans* (Diptera: Culicidae). *Environ. Entomol.* 8:949-955.
- Magnarelli, L. A. 1980. Bionomics of *Psorophora ferox* (Diptera: Culicidae); Seasonal occurrence and acquisition of sugars. *J. Med. Entomol.* 17:328-332.
- Magnarelli, L. A. 1981. Sugar feeding by female tabanids (Diptera: Tabanidae) and its relation to gonotrophic activity. *J. Med. Entomol.* 18:429-433.
- Magnarelli, L. A. 1983. Parity, follicular development, and sugar feeding in *Culicoides melleus* and *C. hollensis*. *Environ. Entomol.* 10:807-811.
- Magnarelli, L. A. 1983. Nectar sugars and caloric reserves in natural populations of *Aedes canadensis* and *Aedes stimulans* (Diptera: Culicidae). *Environ. Entomol.* 12:1482-1486.
- Magnarelli, L. A. and J. F. Anderson. 1981. Sugar feeding by female tabanids (Diptera: Tabanidae) and its relation to gonotrophic activity. *J. Med. Entomol.* 5:429-433.
- Murphy, T. A. and G. R. Wyatt. 1965. The enzymes of glycogen and trehalose synthesis in silk moth fat body. *J. Biol. Chem.* 240:1500-1508.
- Nayar, J. K. and E. Van Handel. 1971. The fuel for sustained mosquito flight. *J. Insect Physiol.* 17:471-481.
- O'Meara, G. F. and E. Van Handel. 1971. Triglyceride metabolism in thermally-feminized males of *Aedes aegypti*. *J. Insect Physiol.* 17:1411-1413.
- Romoser, W. S. and E. Cody. 1975. The formation and fate of the peritrophic membrane in adult *Culex nigripalpus* (Diptera: Culicidae). *J. Med. Entomol.* 12:371-378.
- Van Handel, E. 1965. The obese mosquito. *J. Physiol.* 181:478-486.
- Van Handel, E. 1966. Temperature independence of the composition of triglyceride fatty acids synthesized de novo by the mosquito. *J. Lipid Res* 7:112-115.
- Van Handel, E. 1967a. Determination of fructose and fructose-yielding carbohydrates with cold anthrone. *Analyt. Biochem.* 19:193-194.
- Van Handel, E. 1967b. Non-dependence of the saturation of depot fat on temperature and photoperiod in a hibernating mosquito. *J. Exp. Biol.* 46:487-490.
- Van Handel, E. 1969a. Metabolism of hexoses in the intact mosquito. Exclusion of glucose and trehalose as intermediates. *Comp. Biochem. Physiol.* 29:413-421.
- Van Handel, E. 1969b. The equilibrium reaction sorbitol  $\rightleftharpoons$  fructose in the intact mosquito. *Comp. Biochem. Physiol.* 29:1023-1030.
- Van Handel, E. 1972a. The detection of nectar in mosquitoes. *Mosq. News* 32:458.
- Van Handel, E. 1972b. Simple biological and chemical methods to determine the caloric reserves of mosquitoes. *Mosq. News* 32:589-591.
- Van Handel, E. 1973. Temperature dependence of caloric expenditure and mortality in the starving mosquito. *Comp. Biochem. Physiol.* 44:1321-1323.
- Van Handel, E. 1974. Lipid utilization during sustained flight of moths. *J. Insect Physiol.* 20:2329-2332.
- Van Handel, E. 1975. Direct determination of uric acid in fecal material. *Biochem. Med.* 12:92-93.
- Van Handel, E. and A. O. Lea. 1965. Medial neurosecretory cells as regulators of glycogen and triglyceride synthesis. *Science* 149:298-300.
- Van Handel, E. and A. O. Lea. 1970. Control of glycogen and fat metabolism in the mosquito. *Gen. Comp. Endocrinol.* 14:382-384.
- Van Handel, E. and P. T. M. Lum. 1961. Sex as regulator of triglyceride metabolism in the mosquito. *Science* 134:1979-1980.
- Van Handel, E., J. S. Haeger and C. W. Hansen. 1972. The sugars of some Florida nectars. *Am. J. Bot.* 59:1030-1032.