

Patterns of Lipid Distribution and Utilisation in Insects

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SYNOPSIS. During the course of insect evolution lipids have assumed a significant role in facilitating several important morphogenetic and physiological strategies. Stored glycerides provide a convenient reservoir of metabolic energy for periods of prolonged energy demand, while cuticular lipids are of profound importance in enabling terrestrial insects to resist desiccation.

The present review identifies the lipid classes of fat body, haemolymph and cuticle, and summarises the contribution of lipids to insect development, migration, diapause, protection, reproduction and flight. The release, transport and uptake of lipid during flight is discussed.

INTRODUCTION

The study of insect lipids has received considerable attention in recent years, and a number of reviews have appeared on various aspects of the topic (Scoggin and Tauber, 1950; Strong, 1963; Fast, 1964; Tietz-Devir, 1965; Gilby, 1965; Gilbert, 1967a; Fast, 1970; Gilbert and O'Connor, 1970; Thompson *et al.*, 1973; Gilbert and Chino, 1974). These reviews provide a useful background to the present report which, in compliance with the symposium objectives, identifies the major organs and forms in which lipids are stored, and discusses the significance of lipids in facilitating specific morphogenetic and physiological strategies.

Insects form the most numerous (in terms of individual species) class of living organisms and during their extensive evolutionary history a diversity of morphological, physiological and biochemical adaptations has arisen. This variation requires that caution be exercised in extrapolating for the class on the basis of observations on a few species. However, it is possible to identify certain general characteristics which contribute profoundly to the central role of lipids in ensuring the success of the class:

1) Insects possess a high surface to volume ratio and this, combined with an open

blood system renders them susceptible to desiccation. The ubiquitous distribution of insects is evidence that the potential hazard has been accommodated, and lipids contribute to this alleviation in two ways:

(a) Fats, upon oxidation, yield almost 2 times more metabolic water than carbohydrates, and the storage of energy reserves in the form of fat provides a useful source of non-imbibed water. This additional water assumes particular importance during non-feeding stages in the insect's life history.

(b) The molecular configuration of certain cuticular lipids constitutes the major barrier to water loss and may facilitate absorption of atmospheric water.

2) Active insect flight muscle maintains the highest metabolic rate of any known animal tissue. In order to sustain this energy output for prolonged periods a rich energy source is required, and lipids provide the most efficient and convenient means of storing the required energy. The advantages of lipid over carbohydrate as a metabolic fuel include a higher caloric content/unit weight of substrate, and the fact that triglyceride may be stored in anhydrous form while glycogen is stored in the bulky hydrated form. Thus the use of lipid as a primary metabolic substrate permits accumulation of a large reservoir of energy which may be used during periods of prolonged energy demand.

These considerations are central to the present theme and pertain directly to sub-

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sequent discussion of the importance of lipids in insect life history.

DISTRIBUTION AND FORM OF INSECT LIPIDS

Lipids comprise an essential and integral part of cell membranes in addition to providing an important source of metabolic energy for cell maintenance. As a result lipids can be extracted from all insect tissues. It is beyond the scope of the present report to detail inter- and intra-specific differences in tissue lipids, and in this section discussion will be limited to identification of lipid classes in the three tissues which contain the greatest concentrations of lipid—fat body, haemolymph and cuticle.

Fat body

Insect fat body consists of a diffuse aggregate of cells enclosed by delicate connective tissue membranes. In many insects it extends from the terminal abdominal segment into the head capsule and represents a major component of the haemocoel. Functionally it may be considered analogous to vertebrate liver and adipose tissue, serving not only for the storage of carbohydrate, lipid and protein, but also as an organ of intermediary metabolism (Kilby, 1963).

The storage of lipids in the fat body is well documented and the organ also functions as the primary site of lipid synthesis in the insect (Zebe and McShan, 1959; Tietz, 1961; Bade, 1964; Chino and Gilbert, 1965; Crone *et al.*, 1966; Hirano and Gilbert, 1967; Sun and Brookes, 1968; Thomas, 1974). The dominant lipid class in the fat body of all species which have been examined in this regard is triglyceride, which comprises up to 98% of fat body lipid in pupal and adult *Hyalophora cecropia* (Chino and Gilbert, 1965). Other lipid classes have been detected in the fat body in lesser amounts including diglyceride, monoglyceride, sterols, sterol esters, free fatty acids, phospholipids (Chang, 1974; Thomas 1974; and others), glyceryl ethers (Lambreton, 1972; Tan, 1973); quinones (Lester and Crane, 1959; Laidman and Morton, 1962; Sridhara and Bhat, 1965) and tocopherol (Sridhara and Bhat, 1965). Diehl (1973) has

suggested that oenocytes, which are closely associated with the peripheral fat body of *Schistocerca gregaria* are an important site of paraffin synthesis in that species.

Sexual dimorphism of fat body lipids has been reported in several species (Nelson *et al.*, 1967; Bhakthan and Gilbert, 1972) and changes have also been associated with diet, metamorphosis, reproduction, ageing and exercise (Wigglesworth, 1942; Nelson *et al.*, 1967; Wimer and Lumb, 1967; Sun and Brookes, 1968; Martin, 1969a; Walker and Bailey, 1970; Dutkowski and Ziajka, 1972). These changes serve to emphasize the role of the fat body in responding to varying metabolic and physiological demands.

Haemolymph

Insects possess an open circulatory system in which the haemolymph circulates through a system of body sinuses and directly bathes the various organs. Haemolymph is the primary means by which materials may be transported from sites of absorption or synthesis to storage organs and subsequently to sites of utilisation; consequently the haemolymph lipid profile varies with the physiological state of the animal. Profound changes have been reported during metamorphosis, development, exercise and oogenesis (Beenackers, 1965; Nowosielski and Patton, 1965; Nelson *et al.*, 1967; Mayer and Candy, 1969b; Bollade and Boucrot, 1971; Stevenson, 1972). Lipid concentrations of up to 5.5% have been reported in the haemolymph of some species (Florkin and Jeuniaux, 1973) and this tissue must be regarded as a readily available reservoir of lipid. However, the precise contribution of lipid in this regard cannot be defined until data are available concerning the rate of lipid turnover in haemolymph under a variety of physiological conditions.

In most insects the primary lipid component of haemolymph is diglyceride, with triglyceride and free fatty acids also present (Chino and Gilbert, 1965; Wlodawer and Wisniewska, 1965; Tietz, 1967; Nelson *et al.*, 1967; Mayer and Candy, 1969b; Chippendale, 1971; Stevenson, 1972; Cohen, 1972; Thomas, 1974; Chang, 1974). The he-

mipteran *Pyrhcoris apterus* contains large numbers of triglyceride-containing cells, adipoleucytes, in the haemolymph, and these account for the high haemolymph triglyceride levels which have been reported for this insect (Martin, 1969b). Other lipid classes which have been identified in insect haemolymph include monoglycerides, phospholipids, hydrocarbons, carotenoids and ketone bodies (Nelson *et al.*, 1967; Wang and Patton, 1969; Bridges and Price, 1970; Harashima, 1970; Bennett *et al.*, 1972; Hill *et al.*, 1972; Cohen, 1972; Chippendale, 1973a; Thomas, 1974; Chang, 1974; Diehl, 1975). In addition, the insect hormones, released from the corpora allata and ecdysial glands, are of a lipoidal nature, and are present in the haemolymph at various concentrations during the course of insect development (Gilbert and King, 1973).

Cuticle

Insects are surrounded by a hard outer covering, the cuticle, which provides attachment for muscles and other tissues in addition to preventing or reducing water loss. The cuticle may account for up to 50% of the dry weight of an insect, and as lipids constitute a vital structural and biological component of the cuticle, it is evident that this structure represents an important part of the insect's total lipid content (Locke, 1973; Hackman, 1973).

Much cuticular lipid is present in the form of a stabilised lipoprotein complex, cuticu-

lin, which occurs throughout the cuticle; but little is known about the precise chemical structure of the complex (Wigglesworth, 1970). The major source of cuticular lipid is found, however, in the epicuticular layer which covers almost the entire surface of the insect. From the many studies conducted on various aspects of cuticular lipid composition, it is apparent that considerable interspecific variation exists. Furthermore, the diversity of extraction procedures and analytical techniques employed by various investigators increases the difficulty of defining a typical cuticular lipid profile (see Gilby and McKellar, 1970).

Intra-specific differences in cuticular lipid have been attributed to development (Arnold *et al.*, 1969), sex (Jackson, 1970; Silhacek *et al.*, 1972), seasonal changes (Cavill *et al.*, 1970) and circadian fluctuations (Turner and Acree, 1967). Such variation is to be expected when we consider the critical physiological role of cuticular lipids in enabling the insect to survive different environmental conditions of temperature and humidity.

Table I illustrates the variation in cuticular lipid composition between three unrelated species, and also demonstrates the developmental changes which have been described for two species. It should be noted that in insects, contrary to the situation in most animals, sterol esters constitute only a minor proportion of the total surface lipids (Gilmour, 1965). The developmental changes described for the big stonefly, *Pteronarcys californica*, are of particular in-

TABLE 1. Surface lipid composition of three insects (percentage).

	<i>Pteronarcys californica</i> ^a		<i>Sarcophaga bullata</i> ^b		<i>Periplaneta americana</i> ^c
	Adult	Nymph	New adults	7 day adults	nymph
Hydrocarbons	12	3	53	13	75-77
Wax esters	4	1	3	5	3-5
Triglycerides	7	78	9	20	-
Free Fatty Acids	49	12	26	47	7-11
Sterols	18	1	3	5	<1
Others ^d	10	5	6	10	8-15

^a Arnold *et al.*, 1969

^b Jackson *et al.*, 1974

^c Beatty and Gilby, 1969; Gilby and Cox, 1963; Jackson, 1972.

^d includes alcohols, aldehydes, sterol esters, acidic resins, phospholipids

terest because they reflect a change from aquatic to terrestrial habitat as the animal develops (Arnold *et al.*, 1969). These workers found that the cuticle of the terrestrial adult stonefly contained almost 2 times more extractable lipid than that of the aquatic nymphal stage. This finding is consistent with the earlier reports of Wolfe (cited in Hackman, 1973) who found a reduction in the epicuticular layer of several aquatic insects. The increased hydrocarbon content of adult stonefly cuticle is thought to provide protection against desiccation and it is interesting to note that a similar increase in hydrocarbon is observed in *Sarcophaga bullata* as larvae leave the moist larval environment to emerge as free flying insects (Jackson *et al.*, 1974).

ROLE OF LIPID IN DEVELOPMENT

The complex pattern of insect development and the habitat changes which are often associated with this process result in dramatic physiological and biochemical transformations within a single insect during the course of its life history. The physiology and biochemistry of insect development have recently been reviewed (Chen, 1971; Agrell and Lundquist, 1973) and only salient features pertaining to lipid function will be discussed here. During the development of holometabolous insects there are two non-feeding stages, the embryo and the pupa, and the pattern of lipid synthesis and utilisation during the course of development reflects preparation for these stages.

Embryogenesis

Significant quantities of neutral lipid are deposited in the developing oocyte during oogenesis, and in most species the predominant fraction is triglyceride (Allais *et al.*, 1964; Vroman *et al.*, 1965; Svoboda *et al.*, 1966; Gilbert, 1967b). This fraction declines during embryogenesis and the decrease in glyceride is often accompanied by an increase in phospholipid (Niemierko *et al.*, 1956; Allais *et al.*, 1965; Kinsella, 1966; Kinsella and Smyth, 1966; Gilbert, 1967b; Yurkiewicz and Oelsner, 1969; Lip-

sitz and McFarlane, 1970, 1971). These findings suggest that some glyceride is being used for the synthesis of structural phospholipid while the remainder serves as an energy source for the developing embryo.

Larval development

The lipid content of holometabolous insects increases steadily during larval development although the rate of increase is not constant throughout all larval stages (Gilbert and Schneiderman, 1961; Wimer and Lumb, 1967). Developmental changes have been reported in the relative amounts of the major lipid classes (Wimer and Lumb, 1967; Yurkiewicz, 1970; Castillon *et al.*, 1971; Mauldin *et al.*, 1971) and the fatty acid profile (Sridhara and Bhat, 1965; Nakasone and Ito, 1967; Stephen and Gilbert, 1969; Madariago *et al.*, 1970, 1974; Fernandez-Sousa *et al.*, 1971a, 1971b). These changes reflect not only the metabolic requirements of the larva, but also represent the accumulation of reserves required for maintenance during metamorphosis.

Metamorphosis

Metamorphosis of holometabolous insects involves the breakdown of larval tissues and formation of adult structures. During this stage of development the animal is dependent upon reserves accumulated during larval growth for energy and for provision of anabolic precursors. Lipid and/or carbohydrate may contribute to the energy expenditure of pupae with the relative importance of each substrate dependent upon the species and sex of the animal under investigation (see reviews by Gilbert, 1967a; Chen, 1971; Agrell and Lundquist, 1973). The pattern of lipid utilisation varies during the course of metamorphosis (Ludwig *et al.*, 1964; D'Costa and Birt, 1966; D'Costa and Rutesasira, 1973) with some interconversion of carbohydrate to lipid reported at mid-metamorphosis for two species of blowfly (D'Costa and Birt, 1966; Tate and Wimer, 1974).

ROLE OF LIPIDS UNDER ADVERSE CONDITIONS

One factor which has contributed significantly to the success of insects is their ability to undergo specific physiological and behavioural responses to imminent periods of adversity. The adversity may result from seasonal changes in habitat conditions or it may be caused by a permanent change in the habitat such as would occur in ecological succession. Under these conditions insects may employ one or both of two major strategies to ensure that active stages of morphogenesis occur during optimal environmental conditions. The strategies are *Migration* and *Diapause*, and although the two are not necessarily mutually exclusive, until more precise physiological and endocrinological definitions are available, it is convenient to regard them separately.

Migration

In ecological terms migration is defined as a movement to sites where the next generation can develop or where adults can hibernate or aestivate before flying to another breeding site (Johnson, 1969). The distances involved may be thousands of miles or a few yards and, the significance of lipids in the process is influenced by the nature of the migration.

One of the best documented instances of insect migration is that of the monarch butterfly, *Danaus plexxipus* which enjoys a ubiquitous distribution across the United States and southern Canada during the summer months, but migrates to the southern states and Mexico for winter (Urquhart, 1960). In late winter the insects accumulate large reserves of lipid in preparation for a northerly spring migration, and Cenedella (1971) has estimated that these reserves, which are primarily in the form of triglyceride, are adequate to provide metabolic fuel for the northward migration. Brown and Chippendale (1974) extended this observation to show that adult females can rapidly incorporate glucose into abdominal glycerides, and suggested that dietary sugars may supplement the available triglyceride reserves.

Lipid is also an important substrate for the migratory flights of locusts (Weis-Fogh, 1952). Between 6-8 days after adult emergence the insects enter a period of rapid lipogenesis during which dietary carbohydrate may be converted to lipid and stored in the fat body as triglyceride (Hill *et al.*, 1968; Walker *et al.*, 1970; Walker and Bailey, 1970). The timing of lipogenic activity corresponds to the time taken for adult flight muscle to become fully developed (Brosemer *et al.*, 1963) and presumably, therefore, to the time when migratory flights might be initiated. The lipogenic capacity is retained for up to 20 days and it appears, therefore, that as the migratory swarm feeds, dietary materials are converted into lipid to be used as a substrate for flight.

Karuhize (1972) studied a migratory and a non-migratory species of tettigoniid and found positive correlation between lipid reserves and the inclination of the insect towards flight, a finding which supports the earlier studies of Cockbain (1961) on *Aphis fabae* and Atkins (1966) on *Dendroctonus pseudotsugae*.

Diapause

Diapause is a period of developmental arrest which ensures that the critical stages of morphogenesis are completed in a favourable environment. This strategy does not expose the animal to the risk of failing to find a suitable habitat, as may occur with migration, and is, therefore, particularly useful when the adversity is of a reversible nature (*e.g.* climatic change). Although the stage in which diapause occurs is normally constant within a species, different species may undergo diapause at any developmental stage. Diapause may be likened to a non-feeding stage of development and the event is similarly characterised by a marked accumulation of nutrient reserves prior to its onset (Lees, 1955).

Analysis of the lipid composition of adult face-flies, *Musca autumnalis*, held in reproduction- and diapause-inducing environments from ecdysis, showed that diapausing flies contained 9 times more triglyceride at

15 days, and were still accumulating this reserve after 30 days (Valder *et al.*, 1969). A similar accumulation of lipid by diapausing insects has been reported for *Coccinella septempunctata* (Hodek and Cerkasov, 1961; *Pectinophora gossypiella* (Adkisson *et al.*, 1963) *Anthonomus grandis* (Lambremont *et al.*, 1964) *Hypera postica* (Tombes, 1964), *Trogoderma granarium* (Karnavar and Nair, 1969), *Diatraea grandiosella* (Chippendale, 1973b).

Although hibernation cannot be considered as true diapause, it is interesting to note an accumulation of lipids prior to overwintering in several species (Harwood and Takata, 1965; Heinrichs, 1969; Schaefer and Washino, 1969; Schaefer and Miura, 1972).

ROLE OF CUTICULAR LIPIDS IN PROTECTION

Maintenance of water balance

The migration of animals from water to land required the evolution of effective mechanisms to alleviate the omnipresent danger of dessication. In insects the epicuticular lipid layer presents the main barrier to water loss, and the restricted habitats of those arthropods which are devoid of this layer are testament to the increased potential afforded insects by its presence (Ebeling, 1973). Wigglesworth (1945) and others have demonstrated that removal of the epicuticular lipid layer either chemically or by physical abrasion results in increased water loss with complete dessication evident within a few hours. Beament (1960) extended these observations to demonstrate that it is a thin inner epicuticular lipid layer which is responsible for the impermeability of the cuticle. The chemical and physical basis of the effect is not, however, fully understood (Hackman, 1973).

Cuticular lipids function not only to prevent dessication, but in at least some species they are involved in the absorption of water from moist environments (Beament, 1964). Indeed Collins (1969) has shown that subterranean termites require cuticular absorption of water in order to survive. Again the precise physico-chemical explanation of this effect awaits elucidation.

Pathogens

Koidsumi (1957) demonstrated a pronounced fungicidal action associated with the cuticular lipids of *Chilo simplex* and *Bombyx mori* against cultures of *Aspergillus flavus*. He further showed that removal of cuticular lipids by chemical or mechanical means rendered the insect larvae highly susceptible to attack by muscardines.

ROLE OF LIPID IN REPRODUCTION

As previously discussed, lipids facilitate the process of embryogenesis by providing an efficient source of metabolic energy and an essential source of precursors for the synthesis of cellular and subcellular membranes (Lafon, 1950; Babcock and Rutschky, 1961; Gilbert and Schneiderman, 1961). During vitellogenesis appreciable quantities of lipid are deposited in the eggs (Gilbert, 1967b; Martin, 1969a; Dutkowski and Ziajka, 1972), and in at least some species the source of this yolk lipid is the fat body (Adiyodi and Nayar, 1967; Martin, 1969a; Dutkowski and Ziajka, 1970, 1972). It is possible, however, that in meroistic ovarioles nurse cells may be implicated in the provision of yolk lipid (Falk and King, 1964). Lipid is a constituent of vitellogenin (Dejmal and Brookes, 1968; 1972; DeLoof and DeWilde, 1970) but although extensive studies have been conducted on the nature, transport and uptake of the protein component of this molecule, few data are available concerning the lipid moiety (Dejmal and Brookes, 1972).

ROLE OF LIPID IN FLIGHT

The substrate(s) from which flight energy is derived varies among species, but in many cases the primary source of the required metabolic energy is lipid (Sacktor, 1973). This conclusion is based, in part, upon studies of lipid depletion following prolonged flight in *Euttetix tenellus* (Fulton and Romney, 1940), *Danaus plexippus* (Beall, 1948), *Schistocerca gregaria* (Weis-Fogh, 1952), *Aphis fabae* (Cockbain, 1961), *Dendroctonus pseudotsugae* (Atkins, 1966),

Pantala flavescens (Kallapur and George, 1973) and *Homorocorhyphus nitidulus vicinus* (Karuhize, 1972). These observations combined with reports of fatty acid oxidising enzymes in the flight muscle of some species (Zebe, 1960; Beenakkers, 1963; Domroese and Gilbert, 1964; Bode and Klingenberg, 1964; Thompson and Bennett, 1971; Kallapur and George, 1973) clearly indicate the importance of lipid as a substrate for flight.

Studies on the lipid content of thoracic musculature show that insufficient lipid is present in this tissue to provide energy for extended periods of flight (Beenakkers, 1965; Stevenson, 1972). The muscle must, therefore, derive a continual supply of lipid from the surrounding haemolymph. The haemolymph is in close proximity to individual muscle cells as a result of transverse tubules which penetrate the muscle tissue and into which haemolymph is pumped by working muscle (Weis-Fogh, 1964). Haemolymph diglyceride levels have been shown to change during flight (Tietz, 1967; Mayer and Candy, 1969b; Beenakkers, 1973; Spencer and Candy, 1974) and these observations along with studies on diglyceride turnover (Van Handel and Nayar, 1972) implicate haemolymph diglyceride as an important source of energy for flight muscle metabolism. The use of diglyceride as a source of muscle fuel is of considerable interest and the evolution of this unique strategy has probably contributed to the development of the insect's highly efficient muscular system. It is appropriate, therefore, to consider the mechanism of diglyceride supply and utilisation.

Haemolymph diglyceride is derived from fat body triglyceride with some metabolic rearrangement of the glyceride fatty acid moieties occurring prior to release. Beenakkers and Gilbert (1968) and Beenakkers (1973) demonstrated in *Hyalophora cecropia* and *Locusta migratoria* that the fatty acid complement of haemolymph glycerides differs from that of the fat body. On the basis of these findings they postulated that diglycerides with a specific fatty acid pattern are synthesised in the fat body for release into haemolymph. In locust haemolymph the

concentration of C18:3 is almost twice that found in fat body, while greater concentrations of C16:0 and C18:0 occur in fat body than in haemolymph (Beenakkers, 1973). Fat body contains the enzymes required for desaturation of fatty acids (Tietz and Stern, 1969), and recently Tietz *et al.* (1975) have found a specific 2-monoacyl glyceryl transferase in locust fat body which is thought to synthesise diglyceride from 2-acyl glycerol and free fatty acid. These findings support the proposal that specific haemolymph diglycerides are synthesised in locust fat body from the products of triglyceride hydrolysis.

Studies on several insects have shown that when fat body is incubated in haemolymph, the diglyceride content of the haemolymph rises (Chino and Gilbert, 1964, 1965; Tietz, 1967; Mayer and Candy, 1969a; Downer and Steele, 1972; Thomas, 1974; Chang, 1974). The increased diglyceride levels are not observed if the fat body is incubated in Ringers solution and several studies indicate that a specific haemolymph lipoprotein is required for diglyceride to be released from fat body (Chino *et al.*, 1967, 1969; Thomas and Gilbert, 1968, 1969; Peled and Tietz, 1973). The lipoprotein is synthesised in the fat body, but its release occurs independently of diglyceride release (Peled and Tietz, 1973). The nature of the association between released diglyceride and the lipoprotein is uncertain. Chino *et al.*, (1969) were unable to demonstrate binding of free diglyceride to purified lipoprotein, while Peled and Tietz (1973) found that radiolabelled diglyceride released from fat body *in vitro* does not completely bind to lipoprotein. These findings suggest that the diglycerides released from the fat body, as distinct from that which forms an integral part of the lipoprotein molecule, is weakly bound to the carrier protein. Peled and Tietz (1975) have recently reported a haemolymph protein which enhances incorporation of diglyceride into the lipoprotein, and it is possible that this additional fraction is required for complete binding.

Although diglyceride is the major lipid component of haemolymph in almost all species of insects, triglyceride and free fatty

acid release from fat body have been reported in certain developmental stages of several species (Wlodawer *et al.*, 1966; Cook and Eddington, 1967; Martin, 1969b; Chang and Friedman, 1971; Chang, 1974). Morphological anomalies and/or *in vitro* artifacts may account for some of these observations, but it is probable that in certain species lipid crosses the fat body cell membrane as free fatty acid or triglyceride. Tietz (1967) demonstrated release of free fatty acids from the fat body of flown locusts, but not from rested insects, and free fatty acid release may, therefore, depend on the physiological state of the insect. The requirement of haemolymph to demonstrate *in vitro* release of diglyceride from fat body complicates the interpretation of data obtained from incubation experiments. Lipolytic activity has been reported in the haemolymph of several species (Wlodawer and Baranska, 1965; Chang and Friedman, 1971; Stevenson, 1972; Downer and Steele, 1973; Price, 1975) and a capacity for fatty acid esterification has also been described in this tissue (Wlodawer *et al.*, 1966; Cook and Eddington, 1967; Chang, 1974). Thus the appearance of diglyceride in haemolymph-containing medium may result from secondary lipolytic or esterification processes following an initial release of triglyceride or free fatty acid. However, the demonstration by Chino *et al.* (1969) and Peled and Tietz (1975) that diglyceride is released from fat body into medium containing purified lipoprotein suggests that diglyceride is the primary vehicle of release in at least two species.

The regulation of lipid release from fat body appears to be under neuroendocrine control. Aqueous extracts of corpora cardiaca from *Schistocerca gregaria* cause an elevation of haemolymph diglyceride levels when injected into adult insects, and the hyperlipemia occurs concomitantly with a depletion of fat body triglyceride (Mayer and Candy, 1969a). This finding has been confirmed in *Locusta migratoria* and *Tenebrio molitor* (Goldsworthy *et al.*, 1972b). It is interesting to note that the cockroach, which has little dependence upon lipid for flight metabolism, behaves in an opposite

manner with extracts of corpora cardiaca eliciting a hypolipemic response (Downer and Steele, 1969; Downer, 1972; Goldsworthy *et al.*, 1972b). The importance of neurosecretory influences in locust flight has been demonstrated by Goldsworthy *et al.* (1972a) who sectioned the nerves which transport neurosecretory products from the brain to the corpora cardiaca and found a rapid impairment of flight. Flight capacity was, however, restored by injection of aqueous extracts of the glands. The corpora cardiaca are known to contain several neurohormones (Goldsworthy and Mordue, 1974) and a precise understanding of the mechanism of regulation of lipid release must await purification of the adipokinetic hormone(s).

The nature of uptake of haemolymph lipid by active flight muscle has not yet been elucidated. Diglyceridase activity of moth flight muscle is low (Gilbert *et al.*, 1965; Stevenson, 1969), although an increase in diglyceride lipolysis is evident when the diglyceride substrate is associated with lipoprotein carrier (Gilbert and Chino, 1974). It is also of interest to note that diglyceridase activity is high in the flight muscle of several species which use lipid as a major flight fuel (Crabtree and Newsholme, 1972). Pronounced monoglyceridase activity has been reported in the flight muscle of the moth *Prodenia eridania* and it has been calculated that the activity of this enzyme is sufficient to meet the requirements of flight (Stevenson, 1969). Unfortunately no information is available on the control of muscle lipases, and biochemical observations on lipase activity in isolated tissues or homogenates do not necessarily reflect *in vivo* rates of lipolysis. It is known that the haemolymph diglyceride pool is utilised during flight (Spencer and Candy, 1974), but the mechanism of utilisation will only be resolved by careful analysis of the rates of turnover of individual lipid classes during flight.

CONCLUSION

The present paper has overviewed in very general terms some aspects of the role of lipids in insect life history. No considera-

tion has been given to the significance of changes in fatty acid composition which occur under a variety of physiological and developmental conditions, and the role of lipids as pheromones and hormones has similarly been neglected. These omissions result from the temporal constraints imposed upon the symposium organisers and do not indicate the relative importance of the processes. In this account it has been possible to identify the complexity of insect lipid patterns and to demonstrate the fluctuations in lipid content and form which occur during the life of an insect. These observations show that significant variations in dietary lipid may be found among predators of insects, and indeed the life history strategies of these predators may be influenced accordingly.

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