



## Review

## Lack of lipogenesis in parasitoids: A review of physiological mechanisms and evolutionary implications

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## ABSTRACT

The ability of organisms to adapt to fluctuating food conditions is essential for their survival and reproduction. Accumulating energy reserves, such as lipids, in anticipation of harsh conditions, will reduce negative effects of a low food supply. For Hymenoptera and Diptera, several parasitoid species lack adult lipogenesis, and are unable to store excess energy in the form of lipid reserves. The aim of this review is to provide a synthesis of current knowledge regarding the inability to accumulate lipids in parasitoids, leading to new insights and prospects for further research. We will emphasize physiological mechanisms underlying lack of lipogenesis, the evolution of this adaptation in parasitoids and its biological implications with regard to life history traits. We suggest the occurrence of lack of lipogenesis in parasitoids to be dependent on the extent of host exploitation through metabolic manipulation. Currently available data shows lack of lipogenesis to have evolved independently at least twice, in parasitic Hymenoptera and Diptera. The underlying genetic mechanism, however, remains to be solved. Furthermore, due to the inability to replenish adult fat reserves, parasitoids are severely constrained in resource allocation strategies, in particular the trade-off between survival and reproduction.

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## 1. Introduction

To survive periods of food scarcity, organisms have developed strategies to anticipate these unfavourable environmental conditions. By accumulating energy reserves during periods of food abundance they are able to meet their energetic requirements for survival and reproduction when food is scarce or not available. Energy reserves can be stored in the form of carbohydrates, for example glycogen and other sugars, but those only provide a

short-term energy supply, as the storage capacity for those compounds is limited. A large, long-term, energy source is provided by the lipid reserves, which usually can contain enough energy to last several days to weeks without food. Accumulation of lipid reserves is stimulated by a diet rich in sugars and other carbohydrates (Zinke et al., 2002) or by the expectation of poor nutritional conditions, such as during diapause. During diapause the uptake of additional nutrients is usually restricted or absent and lipids have been found to increase considerably prior to diapause, for instance in the Mediterranean tiger moth, *Cymbalophora pudica* and the cabbage armyworm, *Mamestra brassicae* (Kostal et al., 1998; Ding et al., 2003), as well as other insects (Hahn and Denlinger, 2007).

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The storage of energy reserves in periods of food abundance is typically among the most conserved metabolic responses throughout the animal kingdom. One obvious exception to this rule are species that are not capable of feeding, for instance when adults possess non-functional or no mouthparts. These species do not consume or accumulate any external resource as adults, but instead have to rely on nutrients and energy reserves obtained during the juvenile stages of life. Adult starvation has been shown to accelerate depletion of larval reserves and reduce longevity, fecundity and dispersal in several insect species (Eijs et al., 1998; Shirai, 2006; Gianoli et al., 2007). As a consequence, adult lifespan of non-feeding insects is usually extremely limited and this life

style should be favoured only when no fitness benefits can be gained by an increase in nutritional resources through feeding.

Remarkably, several parasitoid species have also been shown to lack possibilities to accumulate adult energy supplies (Table 1). Although these species are capable of feeding and can utilize dietary nutrients to meet short-term energy demands, they appear to be unable to convert excess carbohydrates to long-term storage in the form of lipids (Ellers, 1996; Olson et al., 2000; Rivero and West, 2002; Casas et al., 2003; Lee et al., 2004a; Fadamiro et al., 2005). Feeding on sugar-rich substrates, such as honey or nectar, does not result in an increase in adult lipid reserves in these species. The physiological mechanisms underlying this inability to

**Table 1**  
Presence and lack of lipogenesis within the class Insecta

Family	Species	Lipogenesis (Y/N)	Parasitic (Y/N)	References
Order Odonata				
Calopterygidae	<i>Calopteryx atrata</i>	Y	N	Matsubara et al. (2005)
Calopterygidae	<i>Calopteryx maculata</i>	Y	N	Marden and Waage (1990)
Order Hemiptera				
Cicadidae	<i>Magicada septendecim</i>	Y	N	Hoback et al. (1999)
Order Orthoptera				
Acrididae	<i>Schistocerca gregaria</i>	Y	N	Chegwidden and Spencer (1996)
Acrididae	<i>Schistocerca americana</i>	Y	N	Hahn (2005)
Gryllidae	<i>Gryllus bimaculatus</i>	Y	N	Lorenz (2001)
Gryllidae	<i>Gryllus firmus</i>	Y	N	Zhao and Zera (2001)
Order Neuroptera				
Nemopteridae	<i>Lertha sheppardi</i>	Y	N	Cakmak et al. (2007)
Order Coleoptera				
Curculionidae	<i>Smicronyx fulvus</i>	Y	N	Vick and Charlet (1996)
Curculionidae	<i>Smicronyx sordidus</i>	Y	N	Vick and Charlet (1996)
Tenebrionidae	<i>Tenebrio molitor</i>	Y	N	Khebbab et al. (1997)
Gyrinidae	<i>Gyrinus opacus</i>	Y	N	Svensson (2005)
Order Diptera				
Culicidae	<i>Aedes aegypti</i>	Y	N	Ziegler and Ibrahim (2001)
Culicidae	<i>Aedes sollicitans</i>	Y	N	van Handel (1965)
Culicidae	<i>Aedes cantans</i>	Y	N	Renshaw et al. (1995)
Culicidae	<i>Aedes punctator</i>	Y	N	Renshaw et al. (1995)
Culicidae	<i>Culex tarsalis</i>	Y	N	Gray and Bradley (2003)
Cuterebridae	<i>Cuterebra austeni</i>	N	Y	Kemp and Alcock (2003)
Scathophagidae	<i>Scathophaga stercoraria</i>	Y	N	Otronen (1995)
Drosophilidae	<i>Drosophila melanogaster</i>	Y	N	Geer et al. (1985)
Tephritidae	<i>Anastrepha serpentina</i>	Y	N	Jacome et al. (1995)
Tephritidae	<i>Ceratitis capitata</i>	Y	N	Warburg and Yuval (1996)
Phoridae	<i>Pseudacteon tricuspis</i>	N	Y	Fadamiro et al. (2005)
Order Lepidoptera				
Saturniidae	<i>Hyalophora cecropia</i>	Y	N	Chino and Gilbert (1965)
Bombycidae	<i>Bombyx mori</i>	Y	N	Horie et al. (1968)
Noctuidae	<i>Spodoptera exempta</i>	Y	N	Lee et al. (2004b)
Sphingidae	<i>Manduca sexta</i>	Y	N	Fernando-Warnakulasuriya et al. (1988)
Nymphalidae	<i>Aglais urticae</i>	Y	N	Pullin (1987)
Nymphalidae	<i>Inachis io</i>	Y	N	Pullin (1987)
Nymphalidae	<i>Danaus plexippus</i>	Y	N	Brown and Chippendale (1974), Gibo and McCurdy (1993)
Order Hymenoptera				
Ichneumonidae	<i>Venturia canescens</i>	N	Y	Casas et al. (2003)
Ichneumonidae	<i>Pimpla turionellae</i>	N	Y	Ortel (1991)
Ichneumonidae	<i>Diadegma insulare</i>	N	Y	Lee et al. (2004a)
Braconidae	<i>Asobara tabida</i>	N	Y	Ellers (1996)
Braconidae	<i>Macrocentrus grandii</i>	N	Y	Olson et al. (2000)
Figitidae	<i>Leptopilina heterotoma</i>	N	Y	Eijs et al. (1998)
Pteromalidae	<i>Nasonia vitripennis</i>	N	Y	Rivero and West (2002)
Eupelmidae	<i>Eupelmus vuilletti</i>	N	Y	Giron and Casas (2003)
Pompilidae	<i>Hemipepsis ustulata</i>	Y	N	Kemp and Alcock (2003)
Sphecidae	<i>Philanthus triangulum</i>	Y	N	Strohm (2000)
Vespidae	<i>Vespa vulgaris</i>	Y	N	Harris and Beggs (1995)
Vespidae	<i>Mischocyttarus mastigophorus</i>	Y	N	Markiewicz and O'Donnell (2001)
Formicidae	<i>Leptothorax albipennis</i>	Y	N	Blanchard et al. (2000)
Formicidae	<i>Camponotus festinatus</i>	Y	N	Rosell and Wheeler (1995)
Apidae	<i>Bombus terrestris</i>	Y	N	Pereboom (2001)

store excess energy in parasitoids, as well as its evolution, have not yet been resolved. The diversity of life histories represented within this group of parasitoids makes it hard to see the adaptive value of this exceptional physiology. Parasitoids, however, are unusual because of their parasitic larval lifestyle, during which the developing larvae can manipulate host metabolism to increase its dietary quality. We propose that the intimate host–parasitoid interaction is one of the physiological processes driving the inability of adult parasitoids to accumulate lipids.

In this review, we will evaluate empirical evidence on the presence and lack of lipogenesis in species within the class Insecta, and discuss novel hypotheses regarding its evolution. The underlying physiological and genetic mechanisms involved in insect metabolism are reviewed, and we evaluate which pathways are potentially relevant to lack of lipogenesis in parasitoids. The physiological interactions between host and developing parasitoid are examined, including their ability to manipulate host resource availability. We, furthermore, set forth the possible implications of lack of lipogenesis for important life history traits.

## 2. Lack of lipogenesis in adult parasitoids

Only a decade ago, it was first noticed that a parasitoid species did not conform to the general metabolic model. In a study by Ellers (1996), general lipid levels of adult parasitoids were compared with lipid levels present after feeding on a sugar-rich diet (Fig. 1). The lipid content of female *Asobara tabida* was highest at emergence and declined monotonically with age, despite continuous *ad libitum* feeding. In starved females, lipid reserves declined even more quickly with age, indicating that access to carbohydrates slowed down the rate of lipid depletion. Hence, lack of lipid accumulation was not due to an inability to consume or digest the food, but to the inability to convert excess carbohydrates to long-term lipid storage. Several other parasitoid species have since also been shown to lack lipogenesis, including *Leptopilina heterotoma* (Eijs et al., 1998), *Macrocentrus grandii* (Olson et al., 2000), *Nasonia vitripennis* (Rivero and West, 2002), *Eupelmus vuilletti* (Giron and Casas, 2003), *Venturia canescens* (Casas et al., 2003), and *Diadegma insulare* (Lee et al., 2004a). These parasitoid species come from a variety of superfamilies within the parasitic Hymenoptera, which demonstrates the widespread occurrence of lack of lipogenesis among adult parasitoid species.

Theoretically, the observed lack of lipid accumulation could be due to an enhanced lipid breakdown, which would remain unnoticed using the experimental design of Ellers (1996). Using radioactively labelled glucose, Giron and Casas (2003) were able to track the fate of incoming nutrients obtained through feeding in the parasitic wasp *E. vuilletti*, and test if the radioactive signal remained confined to carbohydrates and proteins or was transformed to lipids. Their approach demonstrated a rapid increase in body sugar and

body glycogen levels in glucose-fed females. This is consistent with the rise in the level of radioactivity in the extraction phase containing total sugars, and showed that the glucose was indeed digested. More importantly, however, lipid levels never exceeded general levels, and the amount of radioactivity measured in the hydrophobic phase remained very low. These trace experiments confirm the results obtained with feeding experiments: no evidence of *de novo* lipid synthesis has been found in parasitoids under food conditions that would normally induce lipogenesis in other insects (Zinke et al., 2002).

To identify a possible proximate cause of this atypical metabolic behaviour we need to consider more closely the variety of physiological pathways involved in lipogenesis. The primary synthetic pathway in lipogenesis is fatty acid synthesis, which converts the glucose derivative pyruvate to the long-chain palmitic acid (Garrett and Grisham, 1999). The synthesis of palmitic acid is catalysed by fatty acid synthase (FAS), a 250–270 kDa multifunctional polypeptide. A central intermediate in fatty acid synthesis is acetyl coenzyme A (CoA), which is partly carboxylated to malonyl-CoA by the rate-limiting enzyme acetyl-CoA carboxylase. FAS performs the condensation of acetyl-CoA and malonyl-CoA, using NADPH as a reducing equivalent to produce the 16-carbon saturated fatty acid palmitate. The rate of fatty acid synthesis is highly dependent on nutritional conditions. High levels of dietary polyunsaturated fatty acids decrease lipogenesis by suppressing gene expression of fatty acid synthase (Jump et al., 1994). Conversely, a diet rich in carbohydrate stimulates lipogenesis because glucose can be glycolytically converted to acetyl-CoA, which promotes fatty acid synthesis. In *Drosophila* larvae, ingestion of glucose will induce the expression of a number of genes involved in lipogenesis, such as acetyl-CoA carboxylase, acetyl-CoA citrate lyase, and Zwischenferment (Zinke et al., 2002). The cascade of genes involved in lipogenesis makes it difficult to infer which genes are causing lack of lipogenesis in parasitoids without further molecular genetic experiments.

It is clear that FAS has a central role in fatty acid synthesis, which makes it a prime candidate to explain lack of lipogenesis. A mutation in a key position of the FAS gene, or in one of the other genes encoding enzymes involved in fatty acid synthesis, could render it ineffective in synthesizing fatty acids and disable the entire lipid synthesis. Even though it may seem unlikely that a key enzyme like FAS would become dysfunctional or disappear from the genome, recently an example of such evolutionary change was documented in *Malassezia globosa*, a fungus associated with the skin diseases dandruff and seborrheic dermatitis in humans (Xu et al., 2007). Whole-genome analysis showed the absence of a gene encoding fatty acid synthase, explaining *M. globosa*'s dependence on external lipids for growth. No studies have been undertaken on fed adult parasitoids to compare gene expression profiles to other insects that are capable of lipogenesis nor is it known if fatty acid synthesis genes are lacking. A BLAST search of the recently completed *Nasonia* genome (<http://www.hgsc.bcm.tmc.edu/projects/nasonia>) has revealed a homolog to the fatty acid synthase gene of *Drosophila*, however, its functionality remains to be tested. Further genome analysis should enable the identification of evolutionary changes causing lack of lipogenesis; taking into account structural or regulatory changes in FAS and the other enzymes involved in lipogenesis.

The second part of the lipogenesis pathway is modification of saturated long-chain fatty acids to form more complex fatty acids, which are used for the synthesis of various cellular lipids such as phospholipids, triacylglycerols, and cholesterol esters or as precursors in the synthesis of pheromones, waxes, and eicosanoids (Stanley, 2006). Several of the latter compounds are essential to organisms and it is highly unlikely that production of these fatty

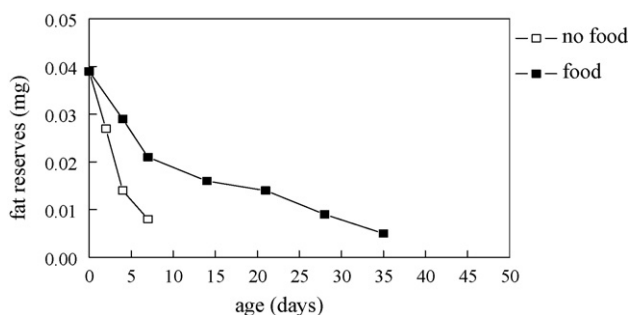


Fig. 1. Decline in lipid reserves (in mg) throughout adult life (in days) in honey fed and starved females of *Asobara tabida*. Graph reproduced with permission of BRILL.

acid derivatives is affected by lack of lipogenesis. The same holds true for the production and modification of phospholipids, which are an essential part of cell membranes for all organisms. Elongation and unsaturation of phospholipids are part of the homeoviscous adaptation of membranes to changing temperature (Hazel, 1995). Observations indicate that these functions are not altered in parasitoids, which suggests that elongases and desaturases are functioning normally. The final step in the lipogenesis pathway is the storage of fatty acids in the insect fat body in the form of triacylglycerols, which consist of three fatty acids and one glycerol molecule. In *Drosophila*, fat storage is regulated by a number of antagonistic enzymes including lipid storage droplet protein *lsd2* (Teixeira et al., 2003), and the lipase Brummer *bmm* (Grönke et al., 2005). Because the mechanisms guiding fat storage are conserved across taxa, parasitoid homologues are expected, but have not yet been identified. Further scrutiny of the *Nasonia* genome could offer useful insight into such homologues in parasitoids.

In summary, the evidence suggests that adult parasitoids do not synthesize fatty acids *de novo*. Analogous to other taxa, this inability could possibly be due to a mutation of a key enzyme in the fatty acid synthesis pathway, but this possibility remains to be examined further. The implications of such an evolutionary scenario are far-reaching; for instance, it would implicate that parasitoids are completely dependent on larval lipid resources as adults. It, furthermore, raises the question as to how larvae accumulate these lipid resources, if key enzymes are rendered dysfunctional. Is endogenous lipogenesis lacking in larvae as well, so that they are entirely dependent on exogenous lipogenesis? An important constraint is the confinement of larvae to a single host. It may, therefore, be crucial to take into account host–parasitoid interactions with regard to nutrient dynamics of both host and parasitoid to understand how adequate lipid levels can be obtained during larval life.

### 3. Larval lipid accumulation strategies

Parasitoids have evolved a complex array of nutritional, physiological, and behavioural interactions with their host (Pennacchio and Strand, 2006). Because the growth and survival of parasitoid larvae is largely dependent on host quality, parasitoids have to ensure a suitable environment for their developing offspring by manipulating their host's development. For instance, koinobionts, allowing host growth and development, can alter host hormone titers to influence the feeding habit and growth of their host (Alleyne and Beckage, 1997; Schafellner et al., 2007). Similarly, idiobionts, which arrest host development, are capable of increasing the duration of paralysis prior to death, allowing for a longer time period and optimal use of host resources (Rivers and Denlinger, 1995). Parasitoids are also capable of manipulating the physiology of their hosts to increase the nutritional composition, which will be our focus in the next section to answer the question of larval lipid accumulation.

Parasitism has been found to induce changes in the amount of amino acids, proteins, pyruvate and carbohydrates within the host in both endo- and ectoparasitoids (Rivers and Denlinger, 1994; Bischof and Ortel, 1996; Coudron et al., 1997, 1998; Nakamatsu et al., 2001; Cònsoli and Vinson, 2004; Caccia et al., 2005). The effects of parasitization on host lipids include an increase in whole body lipid content (Rivers and Denlinger, 1994, 1995), an enhanced metabolism of fat body triacylglycerols (Nakamatsu and Tanaka, 2003, 2004), and a higher level of free fatty acids in the hemolymph. The effects of host manipulation depend on the stage of the developing parasitoid larva, because usually in the early stages the larva mainly consumes host hemolymph, while later the

larva feeds directly on the host's fat body (Nakamatsu et al., 2002; Salvador and Cònsoli, 2008).

These changes in the nutritional content of the host are brought about by a variety of mechanisms such as teratocytes, venom, and associated mutualistic viruses. Teratocytes are cells derived from the dissociation of the embryonic membrane of parasitoid species of the families Braconidae, Scelionidae, and Platygasteridae (Dahlman, 1990), and of the Chalcidoidea (Pedata et al., 2003). Cells resembling teratocytes have also been found in the family Ichneumonidae (Rouleux-Bonnin et al., 1999). Teratocytes play an important role in nutritional exploitation by parasitoid larvae because they attach themselves to the host's fat body and contribute to its disruption (Suzuki and Tanaka, 2007). Several proteins have been identified, including a teratocyte-specific carboxylesterase, assumed to be involved in the hydrolysis of host lipids (Gopalapillai et al., 2005), a fatty acid-binding protein putatively involved in transport of host fatty acids to the developing parasitoid larva (Falabella et al., 2005), and two collagenases which may attack the collagen sheath surrounding the fat body to permit selective release of fat body cells (Qin et al., 2000). In addition to the effects of teratocytes, the parasitoid larva itself is also capable of bringing about physiological changes, for instance in hormone and lipid levels, aiding its own development (Rivers and Denlinger, 1995; Beckage and Gelman, 2004).

Maternal substances, which are transferred along with the egg during oviposition, provide an additional way of host exploitation. These include different types of viruses such as polyDNAviruses, non-polyDNAviruses, and virus-like particles, which are found most frequently in ichneumonoid and braconid wasps (Lawrence, 2005), as well as venom. Parasitoid venom contains various proteins that may disrupt the host's fat body, such as matrix metalloproteinase present in venom of *Euplectrus separatae*, causing lysis of cells and release of lipid particles from the fat body (Nakamatsu and Tanaka, 2004). Also, envenomation leads to increased lipid levels in the host's fat body and hemolymph (Rivers and Denlinger, 1995).

The multitude of mechanisms employed to manipulate host metabolism ensures an abundance of lipid resources during development, providing parasitoid larvae with a unique opportunity to consume host lipids instead of synthesizing them *de novo*. Manipulation and consumption of host lipids probably provides a selective advantage for parasitoid larvae, because *de novo* lipid synthesis is energetically expensive. As a consequence, larval lipogenesis is hypothesized not to occur in parasitoids, and, therefore, to be evolutionary redundant. The hypothesis of direct assimilation of host lipids is supported by the fact that several parasitoid species have similar lipid compositions as their host, although this is not true for all species (Thompson and Barlow, 1974). Obviously, elongation and unsaturation of host lipids can alter lipid composition after uptake by the parasitoid. Experiments using radioactively marked glucose could be used to look into larval capabilities of lipogenesis, similar to the study done by Giron and Casas (2003).

Does this mean that parasitoid larvae lack the ability to synthesize lipids *de novo*? Little conclusive evidence exists, and the few available studies are based on experiments with artificial diets. Thompson (1979) found that larvae of *Exeristes roborator* developed into adulthood on a fat-free artificial diet, suggesting larvae are to some extent capable of *de novo* synthesis of lipids. In contrast, larvae of *Itoplectis conquisitor* did not complete development successfully on a fat-free artificial diet (Yazgan, 1972). So far, no species have been tested at both the larval and adult life stage. It seems unlikely, however, that uncoupling of this trait occurs during metamorphosis, and we would thus expect a lack in larval lipogenesis to be concurrent with that in adults. This would



suggest not all parasitoids are incapable of *de novo* synthesis of lipids, since larval lipogenesis has been shown to occur in *E. roborator* (Thompson, 1979).

#### 4. The evolutionary loss of lipogenesis in parasitoids

How can an essential metabolic trait such as lipogenesis have been lost during the course of evolution? Evolutionary theory predicts that a trait can only be lost if there is a selective advantage for individuals without the trait, for example because maintaining the trait bears an energetic cost. Alternatively, traits may be lost if the trait is no longer under natural selection and accumulated mutations do not affect fitness. These two mechanisms may not necessarily exclude one another, however, in that an energetic cost could accelerate the loss of an unnecessary trait. The most well known example of evolutionary loss of function is the loss of ascorbic acid (vitamin C) synthesis in humans, higher primates, guinea pigs, and fruit bats (Chatterjee, 1973; Ohta and Nishikimi, 1999). The inability to synthesize ascorbic acid is due to inactivation of L-gulonolactone oxidase (GLO), the enzyme that catalyzes the terminal step of L-ascorbic acid synthesis. The mutation leading to the loss of such an essential gene was, however, neutral and not lethal because these animals have a high dietary intake of vitamin C. Without further selective pressure the human non-functional GLO gene has accumulated a large number of mutations since it ceased to function approximately 40–50 million years ago (Nishikimi et al., 1994). The inability to synthesize ascorbic acid was lost a second time independently in guinea pigs 20–25 million years ago (Nishikimi et al., 1992), which demonstrates the relative ease with which this trait is lost.

Similar to vitamin C production, lack of lipogenesis may have evolved in an environment rich in lipids, which would have made lipogenesis evolutionary redundant. The opportunity for parasites and parasitoids to exploit and manipulate their host's resources provides them with a lipid-rich environment and could have made lipogenesis a selectively neutral trait prone to mutation accumulation. This hypothesis provides us with a strong prediction as to which species can and cannot synthesize lipids *de novo*. We only expect species that feed on lipid-rich resources and have a continuous availability of lipid supplies to have lost the ability to synthesize lipids during the course of evolution. To our knowledge, these conditions are only met by parasitic species that are able to manipulate their host's resources to a sufficient extent. All other species, which consume resources poor in lipids, or are prone to experience periods of lipid scarcity during life, should rely on synthesis of lipids to prevent starvation. The hypothesis of exploitation of host lipid reserves has empirical support in parasitic bacteria (Fraser et al., 1995; Mushegian and Koonin, 1996), parasitic fungi (Katinka et al., 2001; Xu et al., 2007), and parasitic nematodes (Köhler and Voigt, 1988). The parasitic lifestyle of these species ensures an abundance of lipid resources from the host, which has made *de novo* lipogenesis unnecessary. In all three taxa, this has resulted in the lack of genes encoding fatty acid synthase, uptake of host-derived fatty acids, and a limitation to condensation of exogenous fatty acids with glycerol to produce triacylglycerols. The parasitic fungus *M. globosa* even possesses a unique set of genes encoding lipases and other hydrolases, which enhance the breakdown of host skin lipids (Xu et al., 2007).

In insects, the hypothesis could explain why only parasitoid species seem to forego the ability to accumulate lipid reserves as adults. To substantiate our hypothesis we have looked at the phylogenetic distribution of the cases of lack of lipogenesis that have been reported so far. An extensive literature study across the class Insecta has shown a total of 35 species are able to produce lipids and 11 species showing lack of lipogenesis (Table 1). All

insects that so far have been proven to be capable of synthesizing lipids as adults are non-parasitic and distributed over all the major superfamilies within the insects. In contrast, the species with lack of lipogenesis are confined to the dipteran and hymenopteran parasitoids. Currently available data on the distribution of lack of lipogenesis provide strong support for the release of selection hypothesis, because lack of lipogenesis is only found in parasitoids. Obviously, a full test of the hypothesis would require testing more parasitoid species, preferably those that are phylogenetically independent. Within the insects, parasitoids occur in a number of taxa including Hymenoptera, Diptera, Coleoptera, and even Neuroptera, allowing identification of at least four evolutionary independent transitions. Moreover, an important suborder for testing lack of lipogenesis are the sawflies or Symphyta, which comprise the most basal lineage within the Hymenoptera, in which parasitism is thought to have originated.

Two additional predictions can be derived from our hypothesis. First, because of the independence of the evolutionary events leading to lack of lipogenesis in the different taxa, it is not expected that the same accumulated mutations are causing lack of lipogenesis. Second, mutation accumulation is a runaway process that is not easily reversed (Siddall et al., 1993). A reversion to a fully functional lipid synthesis requires retracing of numerous evolutionary events and is thought to be highly unlikely. Therefore, we expect to find lack of lipogenesis to be evolutionary conserved within genera or families, so that even those species that use plant hosts as a secondary adaptation, such as gall wasps and fig wasps, may lack lipogenesis.

One argument against the evolutionary redundancy hypothesis is the complex life cycle of parasitoids, which are parasitic during larval development but free-living as adults. Lipogenesis may have become redundant in the larval stages but adult parasitoids may experience severe disadvantages of lack of lipogenesis, such as a reduced lifespan and fecundity. Evolutionary loss of lipogenesis could have occurred only in short-lived species that do not benefit from feeding, for example strongly pro-ovigenic species, in which eggs have matured prior to eclosion. Our hypothesis also does not exclude the possibility that some species may have evolved alternative pathways or behaviours that do allow them to counter the disadvantages of lack of lipogenesis by obtaining some extra lipids as adults, especially in long-lived species.

#### 5. Ecological implications of lacking lipogenesis

The inability of adult parasitoids to synthesize fat, limits the amount of lipids available during adult life. Adult parasitoids cannot obtain a sufficient amount of lipids through dietary intake, since their diet consists mainly out of nectar, honeydew, and occasionally hemolymph of their host, all of which contain carbohydrates and proteins, but hardly any lipids (Eijs et al., 1998; Giron et al., 2002; Giron and Casas, 2003). One class of lipids, the sterols, present in small quantities in host hemolymph, have been found to be of importance for egg viability in the parasitoid *E. vuilletti* (Mondy et al., 2006). These lipids, however, cannot be used as a long-term energy source comparable to triacylglycerols. Teneral lipid reserves, therefore, affect many interrelated life history traits, such as survival and fecundity. It has been shown that fat reserves are positively correlated to body size, longevity, and fecundity in parasitoids (Ellers et al., 1998; Eijs and van Alphen, 1999; Colinet et al., 2007). It can, therefore, be expected that there are strong selection pressures optimizing the size of the teneral lipid reserves, which, in turn, shape developmental traits such as host-use efficiency, development time, and body size. In species entering diapause, for instance, an increase in diapause length has been shown to decrease the amount of teneral lipid

reserves (Ellers and van Alphen, 2002). In species lacking lipogenesis, however, survival and reproductive success are determined by both length of the season and the amount of lipids obtained prior to pupation. Similarly, when different host species can be parasitized, host choice could have severe effects on fitness, since different host species might also differ in their nutritional value to the parasitoid, for instance when the parasitoid is more successful in manipulating host physiology in one host species compared to another, as has been shown for *N. vitripennis* (Rivers and Denlinger, 1995).

A major challenge for parasitoids is to optimally allocate their limited resources either to eggs or survival. Resource allocation is dependent on the timing of egg maturation, either before eclosion (proovigeny) or after eclosion (synovigeny), on oosorption ability and on host availability (Olson et al., 2000; Jervis et al., 2008). In general, parasitoids appear to be time limited rather than egg limited (Rosenheim, 1996; Ellers et al., 1998, 2000; Sevenster et al., 1998), so that lifetime reproductive success is limited by fat reserves, rather than egg load in the majority of wasp species (Ellers et al., 1998). In species lacking oosorption, allocation of lipids into reproduction will increase the number of eggs and results in decreased plasticity (Ellers and van Alphen, 1997). The inability of parasitoids to accumulate fat reserves as adults implies they are severely constrained in resource allocation strategies, in particular the trade-off between survival and reproduction.

According to Boggs' model (1981) on nutrient dynamics and resource allocation in insects, the amount of nutrients that can be obtained during the adult life stages determines allocation to reserves at hatching. In addition, biochemical research has shown that insects maintain separate nutrient pools for essential and non-essential nutrients, which fuel different functions, and, therefore, not only the amount of nutrients is of importance, but also which specific nutrients can be obtained (O'Brien et al., 2002). If we would apply this model to lipogenesis in parasitoids, it would be expected that long-lived species are capable of lipogenesis and eclose with relatively few lipids, as opposed to short-lived species, which have accumulated a sufficient amount of nutrients to sustain throughout the adult life stage.

## 6. Conclusions

We have provided an overview of current knowledge on lack of lipogenesis and its effect on several aspects of parasitoid biology. Parasitoids are prone to lose the capability of lipid synthesis because of their ability to exploit host nutritional resources, but it is unsure if all parasitoids lack lipogenesis and what the exact physiology is. Future research should follow several leads, including the identification of additional parasitoid species within major superfamilies of Hymenoptera, Diptera, and Coleoptera with lack of lipogenesis, which will allow us to determine how many times lack of lipogenesis has evolved independently within these groups and if it is present in all parasitoid lifestyles. Furthermore, the underlying physiological and genetic pathways that are involved in lack of lipogenesis in parasitoids should be identified, both in larva and adult parasitoids.

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